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ENTOMOPHAGOUS INSECTS

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BY

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PREFACE

This has been termed the age of insects, and it has been said that they are the chief competitors of man for possession of the earth. As in the case of the human race, however, the insects are their own worst enemies, and it is to this relentless conflict that we owe a large measure of credit for the maintenance of equilibrium in the insect population at a sufficiently low level to permit of the existence of plant and animal life as we know it today. The entomophagous insects comprise a very considerable portion of the total insect population, as is readily realized when we consider that the great majority of species of other food habits have one or more species of parasites or predators which live at their expense.

Ever since the early days of entomology, when the study of habits followed the early attempts at classification of the adult insects, the phenomenon of one insect preying upon another and being dependent upon it for food has attracted attention. The latter half of the nineteenth century was productive of a great advance in our knowledge of this phase of entomology and the foundation was then laid for what we now call biological control, the utilization of parasites and predaceous insects in the control of crop pests. This method is generally recognized today as one of the promising lines of approach to the solution of a great many of our major insect problems.

The literature dealing with entomophagous insects is assuming formidable proportions, and the fieldworker or student has access to only an exceedingly small fraction of the publications relating to the subject. He is consequently unable to familiarize himself with the important contributions that have appeared in many countries and languages. The present volume represents, as nearly as possible, what the author himself would like to have had available while engaged in field work upon insect parasitology and the biological control of insect pests.

In the discussion of the biology and habits of the entomophagous insects, particular attention has been given to those groups which reveal a high degree of specialization in their host relationships and in the form of the immature stages to adapt themselves to this mode of life. The generalized predators, consequently, are dealt with briefly and only sufficiently to illustrate the host preferences and habits of each group.

It is with particular pleasure that the author expresses his appreciation to all of those who have contributed in various ways to the preparation of this book. First, to Prof. Harry S. Smith of the University of California, under whom the author served his apprenticeship and who has been a constant source of encouragement and advice since that time. Many members of the staff of the Bureau of Entomology and Plant Quarantine have given invaluable assistance. C. F. W. Muesebeck and the specialists of the Division of Insect Identification have made determinations of a number of species and have reviewed the manuscript informally. In justice to them, however, it should be stated that the groupings and names used do not always represent their opinions and are the author's own responsibility. Grateful acknowledgments are made to the staff of the Bureau library and to Carlo Zeimet, translator, J. G. Pratt, photographer, and Mrs. M. F. Benson, artist. Much of the laborious clerical work in the preparation of the manuscript was done by Miss L. L. Bennett, to whom many thanks are extended. Dr. S. E. Flanders of the University of California has kindly reviewed the section dealing with the Aphelinidae. The courtesy of J. D. Maple and D. W. Clancy in permitting inclusion of data and illustrations from unpublished manuscripts is particularly appreciated.

Thanks are extended to the many authors whose illustrations have been used, each of which is credited in the legend accompanying the figure.

CURTIS P. CLAUSEN.

WASHINGTON, D. C.,
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ENTOMOPHAGOUS INSECTS

The habit of feeding upon other insects is found in all the major orders of insects. It ranges from incidental feeding during times of scarcity of the normal food to obligate parasitism. The latter involves development upon a limited number of host species, and in occasional instances it extends to actual specificity. Sweetman (1936) lists 87 families, in 5 orders, which contain species of parasitic habit, while those which are predaceous are included in 167 families, representing 14 orders. Allowing for duplications in the two lists, there are 224 families, in 15 orders, which have adopted, in some measure, the entomophagous habit.

A consideration of the relationships between entomophagous insects and their hosts requires the employment of certain terms to designate specific relationships. These insects are broadly divided into two general classes, the parasites and the predators. The term parasite, in medical and veterinary entomology, has a very different meaning from that which it has in insect parasitology, and there appears to be little possibility of reconciling the two, nor is there any real need for doing so. When applied to an entomophagous insect, it refers to one that, in its larval stage, develops either internally or externally upon a single host individual, the latter eventually dying as a result of attack. The adults are, with very few exceptions, free-living, and their food sources are usually distinct from those of the larvae. A predator, on the contrary, is to a large extent free-living in the larval stage also; it kills the host immediately by direct attack and requires a number of individuals to provide sufficient food to bring it to maturity. The predator is of greater size than the prey, and the food sources of the adults and immature stages are often the same. Many instances might be cited of particular species that are intermediate between the two or that fail to meet entirely even the broad definitions given. No sharply defined line of demarcation can be drawn between the two.

It has been mentioned above that the food sources of the adults of parasitic insects usually differ from those of the immature stages, whereas among the predators they are usually the same. The greatest divergence in feeding habits of the adults and the larvae or nymphs is found in a few species that have parasitic or predaceous larvae, yet the adults are strictly phytophagous and are classed as crop pests.

In referring to a species or group as being parasitic or predaceous in habit, it should be borne in mind that it is the immature stages which are referred to unless otherwise specified.

The first effort to define the relationships between a host and its parasites and between the parasite species themselves was made by H. S. Smith (1916), and several later authors have proposed modifications or entirely new series of terms to designate the different relationships. The latter have, in part, some merit; but Smith's definitions are generally understood and are adequate for present purposes. There are, however, two general terms in wide use for which the distinction should be pointed out. "Host preferences" relate, as the term implies, to the choice of

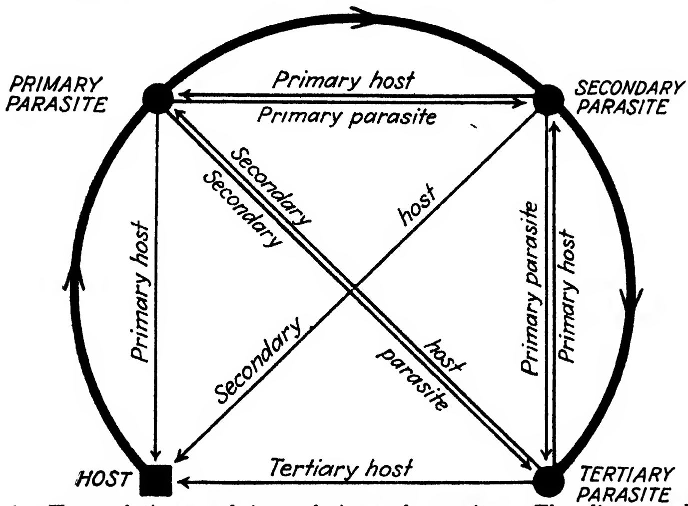


Fig. 1.—Host relations and interrelations of parasites. The diagram shows the relationship between any two and all species in a complex consisting of a host insect and parasites of the first, second, and third degree.

host species for attack, and under that heading we list the insects that are the normal hosts of species or higher groups in nature. "Host relationships," on the contrary, refer to the direct physical relationship between an individual parasite or predator and the individual host. The latter term is often erroneously used to cover the first as well.

In the discussion of the parasite complex associated with a given insect, there is often considerable confusion because of uncertainty or ambiguity in expressing the relationship between particular members of the series. This is especially true where the parasite series extends to the third degree. In Fig. 1, an attempt has been made to show in diagrammatic form the relationship between any two members of such a series. The third member, which is a tertiary parasite of the species designated as the host of the series, is a primary parasite of the secondary; and, conversely, the latter is its primary host.

HYMENOPTERA

The Hymenoptera are the dominant order among the entomophagous insects, both as regards the number of species having that feeding habit and in the frequency and effectiveness with which they attack the insect pests of agricultural crops. About half the families having entomophagous representatives are strictly parasitic in habit, one-fourth are predaceous only, and the remainder contain both parasites and predators. The most important and frequently encountered families of parasitic habit are the Ichneumonidae and Braconidae, which attack a wide variety of caterpillars, sawfly larvae, beetle larvae and adults, etc. The Encyrtidae and Aphelinidae are generally encountered as parasites of Homoptera, whereas the Scoliidae and Tiphiidae limit themselves to the grubs of Scarabaeidae. The Trichogrammatidae, Mymaridae, and Scelionidae are parasites of eggs only. In a great number of the families, a varying portion of the species is of hyperparasitic habit, this being particularly evident in the Ichneumonidae, Eulophidae, and Pteromalidae. The Formicidae are probably the most important of the predaceous groups and possibly of the entire order. Because of the exceedingly wide range of host preferences within the order, a detailed statement of this subject is not presented here but is included in the discussion of the respective superfamilies and families. There are, however, several biological topics that may be discussed with reference to the order as a whole, and an enumeration and description of the different egg and larval forms are also given below.

PLACEMENT OF THE EGG IN RELATION TO THE HOST

There is a great variety in the manner and place of oviposition by the Hymenoptera, ranging from the common internal placement of the egg to its deposition on foliage or in plant tissue far removed from the host. These variations in habit are often correlated with adaptations in form or structure of the egg, and they presumably serve a definite purpose, though frequently the relationship is not obvious. The following outline presents the different positions in which the eggs may be placed, with examples of species or groups having each habit.

A. Internal parasites, the egg deposited internally,

1. In egg of host, to develop in a later stage. (Several genera of Braconidae, Encyrtidae, and Platygasteridae, and occasional species of Ichneumonidae, Callimomidae, Eulophidae, and Cynipoidea.)

2. Free in the body cavity of the larva, pupa, or adult.
   a. In that of the primary host. (Of general occurrence.)
   b. In that of the primary host within the living secondary host. (*Mesochorus* spp., *Brachymeria dalmani* Thoms., *Aphidencyrtus aphidivorus* Mayr, etc.)
3. Regularly placed in a particular organ.
   a. In the brain or a ganglion. (Several Encyrtidae and Platygasteridae.)
   b. In the intestine. (*Platygaster zosine* Wlk., *Diversinervus elegans* Silv., *Microterys clauseni* Comp., etc.)
   c. In the embryo while still within the parent female. (Not definitely known to occur, but probable.)
4. Attached to the body wall.
   a. By its stalk fixed in the oviposition puncture in the host integument. (*Encyrtus*, *Microterys*, and other genera of Encyrtidae.)
   b. By an "adhesive disk" to the inner body wall. (*Therion morio* F. and *Heteropelma calcator* Wesm.)

B. Internal parasites, the egg deposited externally,
1. In contact with the host. (*Eretmocerus serius* Silv. and *Coccophagus ochraceus* How.)
2. Partially embedded in a puncture in the host integument. (Occasional in several species of Dryinidae.)
3. Entirely apart from the host. (All Trigonalidae, and *Orasema* spp.)

C. External parasites, the egg deposited externally,
1. Adhering to the host integument. (Of general occurrence.)
2. Attached to the host integument.
   a. Partially embedded in a wound in the host integument. (*Anisoctenion alacer* Grav. and several species of *Exenterus*.)
   b. The tip of the pedicel or stalk inserted in a puncture in the host integument. [Agriotypidae, many tryphonine Ichneumonidae, and occasional species of Eulophidae (*Elachertus* and *Euplectrus*) and Aphelinidae (*Euxanthellus* and the male eggs of several *Coccophagus*.)]
3. In immediate vicinity of host in cocoon, cell, burrow, etc. (of general occurrence).
4. Entirely apart from the host. (The great majority of Eucharidae and the parasitic Perilampidae.)

EGG-LARVAL PARASITES

Under this heading we include a relatively large group of parasitic Hymenoptera, distributed through a number of families, which oviposit in the host egg but complete their development in the larva or pupa. They are all true larval parasites in the sense that their development is primarily at the expense of that stage. Species having this habit are often referred to as egg parasites, but there is no more justification for so terming them than to designate a tachinid species an external parasite merely because its egg is deposited externally upon the host. So far as known at present, the above manner of oviposition and development is found only in the Hymenoptera, though in four superfamilies. These are the Ichneumonoidea (Ichneumonidae, Braconidae), Chalcidoidea (Encyrtidae, Callimomidae, Eulophidae), Cynipoidea (Ibaliinae), and Serphoidea (Platygasteridae). Oviposition in the egg, with development

in and emergence from a later host stage, was first suggested by Kirby in 1800, in the case of *Isostasius inserens* Kirby, a parasite of *Phytophaga*. Investigations since that time have substantiated this conclusion and have revealed that the habit is common to many members of the family Platygasteridae, though some of them will also attack the newly hatched larvae. All of these which have been studied in detail are parasites of the Cecidomyiidae, and the adults emerge either from the mature larva or from the puparium.

In the Cynipoidea, the single recorded instance of the above oviposition habit is for *Ibalia leucospoides* Hoch., which is parasitic in *Sirex*. In this species, oviposition may be in either the egg or the newly hatched larva and the host is killed in its late larval stage.

Among the Ichneumonidae, *Collyria calcitrator* Grav. oviposits in the egg of its sawfly host and completes its development in the mature larva, and *Sagaritis dubitatus* Cress. questionably has the same relationship to its lepidopterous host. Perhaps the best known representative of the family is *Diplazon laetatorius* F. and others of that genus, which oviposit either in the egg or in the larva of various Syrphidae, the adult emerging from the puparium. In the Tryphoninae, *Oocenteter tomostethi* Cush. places its egg in that of the host, and development is completed in the mature larva.

The Braconidae have a considerable number of species, particularly of the genera *Chelonus*, *Ascogaster*, and *Phanerotoma*, which oviposit in lepidopterous eggs and complete their development in the larvae. The habit is consistent in these genera. Several species of *Microgaster* attack lepidopterous hosts in the same way, and an occasional species of *Coelinidea* and *Sympha* oviposit in the eggs of their dipterous hosts and emerge from the puparium.

Among the Chalcidoidea, the family Encyrtidae contains a considerable number of species of *Ageniaspis*, *Copidosoma*, and closely related genera, which deposit their eggs in those of Lepidoptera and complete their development in the later stages. These comprise principally the species of polyembryonic habit. *Tetrastichus asparagi* Cwfd. places its eggs in those of the asparagus beetle, and maturity is reached only after the host larva has completed its feeding and formed the pupation cell in the soil. *Epimegastigmus brevivalvus* Gir. oviposits in the egg of *Megastigmus* and kills the host in its mature larval stage.

It is of interest that most if not all of the polyembryonic representatives of the Encyrtidae and Platygasteridae have the egg-oviposition habit, and this may possibly be explained by the longer period required for embryonic development. That requirement is lacking in the isolated instances occurring in other families. Thus *T. asparagi* represents a

striking departure in habit from other members of the same genus that attack similar hosts.

It has been mentioned that the dipterous hosts of some of the species referred to form the puparium before death, and occasional individuals of other species may likewise do so. This represents the final activity of the host, and death follows very quickly and without the attainment of the perfect pupal stage.

UNISEXUAL REPRODUCTION

The production, under normal conditions, of female progeny generation after generation without the intervention of the male is of much more frequent occurrence among the parasitic Hymenoptera than in other orders of entomophagous habit. Rather surprisingly, it has not yet been found to occur in the Serphoidea. In no family or even genus is the habit of general occurrence, and it is apparently a specific adaptation to meet particular conditions.

This manner of reproduction has been recorded in one or more of the entomophagous species of the following families and genera.

Ichneumonoidea:
- Braconidae (*Apanteles, Chelonus, Microctonus, Rogas*).
- Ichneumonidae (*Hemiteles, Nemeritis, Polyspincta*).

Chalcidoidea:
- Mymaridae (*Anagrus, Paranagrus, Polynema*).
- Trichogrammatidae (*Trichogramma, Oligosita*).
- Eulophidae (*Tetrastichus, Ootetrastichus, Pleurotropis, Thripoctenus*).
- Aphelinidae (*Aphelinus, Aphytis, Encarsia, Prospaltella*).
- Encyrtidae (*Achrysopophagus, Adelencyrtus, Anagyrus, Blepyrus, Habrolepis, Pauridia, Saronotum*).
- Eupelmidae (*Anastatus, Eupelmus, Eupelmella*).

Vespoidea:
- Bethylidae (*Sclerodermus*).
- Dryinidae (*Gonatopus*).

In the majority of species which reproduce unisexually, and of which sufficiently large rearings have been made, it has been found that occasional males appear. These may be degenerate forms incapable of mating or normal and able to accomplish mating readily. In the latter case, however, the progeny are again all female.

It has been recorded by Phillips and Poos (1921) that the spring brood of *Ditropinotus aureoviridis* Cwf. consists solely of females, whereas the progeny of these include a small proportion of males. The same authors (1927) state that virgin females of *Eridontomerus isosomatis* Riley produce progeny of both sexes.

POLYEMBRYONIC REPRODUCTION

Among insects the development of two or more individuals from a single egg has been demonstrated thus far only in the Hymenoptera, though in that order it occurs in no less than four superfamilies and a number of genera. as follows:

Hymenoptera.
- Ichneumonoidea.
  - Braconidae (*Macrocentrus* spp.).
- Chalcidoidea.
  - Encyrtidae (*Ageniaspis*, *Litomastix*, *Copidosoma*, etc.).
- Serphoidea.
  - Platygasteridae (*Platygaster* spp.).
- Vespoidea.
  - Dryinidae (*Aphelopus theliae* Gahan).

The literature dealing with polyembryonic reproduction in the Hymenoptera is becoming quite extensive. The embryological phases of the subject are too complex to permit of adequate treatment here, but the references cited in the discussion under the respective families may be consulted if detailed information is required. Several general reviews on the subject have been published, among which may be mentioned those of Howard (1906), Gatenby (1918), Leiby (1929), and Silvestri (1937).

In reviewing the host preferences of the various groups of polyembryonic habit, an exceptional consistency becomes evident. The Braconidae and Encyrtidae develop in Lepidoptera only, whereas the Platygasteridae parasitize the dipterous family Cecidomyiidae. Only in the Encyrtidae is more than one genus known to have this habit, and the several genera of that family are closely related and, being of common origin, naturally would show a consistency in host preferences.

Deposition of the egg in that of the host, together with the completion of larval development in the mature larva or pupa of the latter, is the habit of all polyembryonic Encyrtidae and Platygasteridae. A maximum period of time is consequently available for embryonic development; and this, as well as other undetermined requirements, has brought about the adoption of a habit that is uncommon among the species of the same families that reproduce monembryonically.

The number of individuals that are able to develop to maturity in a single host is, of course, in direct proportion to the size of the mature host larva, as the entire body contents are consumed by the parasite brood. Very frequently the number of young larvae present in a host is larger than the food supply can support and the surplus consequently die and are themselves consumed. The broods of *Macrocentrus gifuensis*

Ashm. in *Pyrausta nubilalis* Hbn. range from 16 to 24, whereas in *M. ancylivorus* Roh., which develops in larvae of *Grapholitha molesta* Busck, only a single individual emerges, even though the early stages of embryonic development show numerous morulae, germs, and pregerms, and several may even attain the first larval stage. Daniel (1932) expresses the belief that the latter species, at one period in its development, was parasitic in a host of greater size than *Grapholitha*, in which polyembryonic reproduction was successfully accomplished.

All the polyembryonic Encyrtidae are exceedingly small, though a number of them attack large hosts, and consequently the number that can reach maturity in a single caterpillar is very large. The maximum recorded is somewhat more than three thousand from a larva of *Phytometra brassicae* Riley.

The hosts of the Platygasteridae are of smaller size, and the number of *Platygaster* produced in cecidomyiid larvae ranges from only 2 to 18.

The habits of the polyembryonic *Aphelopus theliae* differ in several respects from those of other groups of similar habit. The egg is deposited in nymphs of any of the first three instars of the membracid host, and death of the latter takes place in the last nymphal or the adult stage. Forty to sixty individuals develop to maturity in each host. As in *Macrocentrus*, the mature larvae emerge from the host body for pupation.

The large numbers of individuals mentioned above from single hosts are not invariably, or even generally, the product of a single egg. Some species consistently deposit a single egg at each insertion of the ovipositor, whereas others deposit two or more. In *Copidosoma* and *Litomastix*, which produce the largest numbers, each egg may give rise to one or two thousand larvae, but the larger broods are quite consistently the product of a number of eggs from one or several parasite females.

The parasite brood from a single host may all be of one sex or it may comprise both sexes. There is a marked difference between species in this respect, as shown below:

Parasite	Approximate number per brood	Per cent male broods	Per cent mixed broods	Per cent female broods
Macrocentrus gifuensis	16–24	35.5	37.5	27.0
Copidosoma gelechiae	160	37.0	1.0	62.0
Litomastix floridanus	1,000–2,000	3.9	83.7	12.4
Litomastix truncatellus	1,000–2,000	11.3	87.0	1.7
Platygaster felti	11–18	0.0	95.0	5.0
Platygaster hiemalis	6	0.0	80.0	20.0
Platygaster variabilis	15	0.5	92.0	7.5

It is seen that mixed broods are greatly in the majority in *Litomastix* and *Platygaster*, whereas *C. gelechiae* is distinctive in having a preponderance of pure female broods, with mixed broods occurring only rarely.

The origin of mixed broods has been the subject of extensive study, particularly by Patterson (1917, '19, '21*b*) and Leiby (1926). It had originally been assumed that mated females produce only female progeny and virgin females only male progeny and that mixed broods consequently arise from oviposition by both mated and virgin females in the same host egg. It has since been shown by Leiby that in *L. truncatellus*, which deposits one or two eggs at each insertion of the ovipositor, 80 per cent of the paired eggs deposited by mated females showed one with a sperm and the other unfertilized. His conclusion that the female can and does control the fertilization of her eggs at the time of deposition is supported by the recent studies by Flanders (1939) on other parasitic insects.

Patterson believes that both sexes may develop from fertilized eggs and males only from unfertilized eggs. In the former case, the appearance of males is attributed to an abnormal behavior of the sex chromosomes. In *P. felti*, which produces 11 to 18 in each brood, 60 per cent of the mixed broods included only a single male, and in none did the number equal that of the females.

The determination of the polyembryonic mode of reproduction in these minute parasitic Hymenoptera requires a thorough knowledge not only of embryology but of cytological technique, and it is therefore not surprising that the number of entomologists who have conducted researches upon the subject is small. It is probable that further investigation will appreciably extend the range of occurrence of the habit in the Hymenoptera. There are several additional genera of Encyrtidae and Platygasteridae in which it is suspected, and a further extension may be looked for in the Braconidae.

Among the gregarious parasites, polyembryonic reproduction may be suspected where a combination of the following features in the biology of a species is encountered: (1) oviposition in the egg or very young larva of the host, with maturity attained in the mature larva, pupa, or adult; (2) exceptionally large numbers of progeny developing in a single host; (3) simultaneous development and emergence of the brood; and (4) a portion of the broods consisting of one sex only, and the mixed broods showing a wide variation in sex ratio.

The reproductive potentials of polyembryonic Hymenoptera are in some instances exceedingly high, whereas in others it does not exceed that of monembryonic species of the same family. The maximum is found in the genus *Litomastix*, which may produce up to two thousand progeny from a single egg. Several eggs are usually deposited at each

insertion of the ovipositor, and the great preponderance of mixed broods and the general occurrence of several embryo chains in each host indicate that multiple oviposition is normal. With an average deposition of 75 eggs per female and on the assumption of an average production of 500 progeny from each egg, there is the possibility of a female giving rise to nearly forty thousand progeny. These species have a relatively low egg capacity as compared with others of the same family.

A marked contrast in reproductive capacity is found in *Platygaster hiemalis* and *P. zosine*, both parasites of the hessian fly in North America. The ovaries of gravid females of *P. hiemalis* contain an average of 3,300 eggs, and each one gives rise to one or two individuals. The possible number of progeny is consequently in the neighborhood of five thousand. In *P. zosine*, an average of only 228 eggs is produced, and each one may develop into 2 to 12 individuals, the average being 7.9. On this basis the total progeny would be approximately eighteen hundred. The two species attain approximately the same percentage of parasitization under field conditions.

Polyembryonic development results in an increase of varying extent in the reproductive capacity, but it does not necessarily confer a corresponding advantage or increased efficiency upon the species in which it has arisen. It may be viewed, instead, as an effort on the part of each one, not altogether successful in most instances, to overcome the particular limiting factors that operate against it. The records of field parasitization indicate that relatively few of these species are able to attain an effective status and that the percentage of hosts destroyed by them is usually relatively low even in high populations.

The fact that oviposition takes place in a very early stage of the host, usually the egg, and that its death is brought about only after larval maturity is attained explains in part the need for a high reproductive capacity. The parasite must provide not only for losses that it suffers directly but also for those of the host during the entire egg and larval period. Host mortality during this time is always exceedingly high, and parasite loss is in a corresponding ratio.

PHORESY

The term phoresy was first proposed by P. Lesne in 1896 to designate the carriage of certain insects by others for purposes not associated with direct feeding. Howard (1927) has reviewed the subject, citing the known instances of this habit, and suggests that it may prove to be of frequent occurrence among parasitic insects, particularly the Scelionidae. Lesne concludes tentatively that in certain groups this habit may represent a stage in the development of a true parasitic habit by the adults

and cites the Hippoboscidae as an illustration of one which may have had its parasitic beginning in that way. With reference to the entomophagous insects, however, we are concerned only with that form of phoresy which involves the association of a parasite or predator with another insect for the purpose of gaining access to the host stage which is to be attacked. This association may be on the part of an adult female parasite attaching herself to a female host for the purpose of attacking the eggs as soon as they are laid, or it may be an instance of the first-instar larva attaching itself to an adult female or worker of a brood-tending host, in which case the larvae are the objects of ultimate attack.

Phoresy on the part of adult parasites is at present known to occur frequently only in the serphoid family Scelionidae, the species of which are parasitic in the eggs of other insects. This habit is advantageous to the parasite in enabling it to attack the eggs immediately after deposition. These species are usually not able to develop in eggs that have undergone any appreciable degree of embryonic development, and consequently the period of time in which they are in a suitable stage for attack is short. Others apparently employ this means to gain access to eggs contained in a thick, tough case through which they are unable to reach the eggs after it is fully dried and hardened. *Rielia manticida* Kieff., a parasite in the eggs of Mantidae, has been studied by Chopard and Rabaud in Europe (see page 251). The female *Rielia* is usually found beneath the wings, laterally upon the meso- or metathorax, or between the genital plates at the tip of the abdomen. As the female mantid is engaged in the deposition of her mass of eggs, the parasite releases her hold upon the body and descends into the frothy mass for the deposition of her own eggs. In this case, the relationship between the parasite adult and its carrier is exceptionally close, as the former apparently feeds upon the body fluids and the death of the latter results also in the death of the parasite. *Rielia* is therefore parasitic in both the adult and the larval stages.

Several authors have observed the presence of *Scelio* and *Lepidoscelio* females upon the bodies of other Orthoptera, particularly grasshoppers. However, the great majority of species of these and related genera attacking the same hosts apparently gain access to the egg masses without the aid of a carrier.

The most interesting account of phoresy among the Scelionidae is that recently presented by Van Vuuren (1935) regarding *Phanurus beneficiens* Zehnt. (see page 251) parasitic in the eggs of *Schoenobius incertellus* Wlk. and other lepidopterous borers of similar habit in Asia. More than one-third of the females observed were attached to the wings of the female moths, and the remainder were mostly upon various parts of the abdomen.

Ghesquiere (1921) observed the presence of adult females of an undetermined serphoid parasite, probably a scelionid, upon the bodies of adult females of a coreid bug, *Anoplocnemis curvipes* F., and noted that as soon as the latter deposited eggs the parasites moved from their previous location and oviposited in them.

Two points are noteworthy in connection with the above records for the Scelionidae: (1) Only female parasites are to be found upon the carriers. (2) Most, and in some cases all, of the parasites are found upon female carriers. The latter is explained by the greater size and possibly greater attractiveness of the females and by their less active life, which gives the parasites greater opportunity for attaching themselves.

The utilization of the insect female as a carrier by the females of species that parasitize their eggs is further illustrated by *Oligosita xiphidii* Ferr. of the family Trichogrammatidae (Ferriere, 1926). The females were found attached to the lower wings of the tettigoniid, *Xiphidion longipenne* de Haan.

The obligatory employment of a carrier by the first-instar larva of a parasite or predator, by means of which it reaches the host stage that is to be attacked, presents several features that differ from those already discussed. Several striking adaptations of this type are known in the hymenopterous family Eucharidae (see page 226), which are parasitic upon the prepupae and pupae of ants. The eggs of the parasites are invariably deposited entirely outside the ant nest, often at some distance. After hatching, the planidia attach themselves to the worker ants and are thus carried into the nest, where they transfer to the larvae or pupae upon which they are to develop to maturity. An undetermined species of *Psilogaster* occurring in Malaya represents the highest development of the habit among the parasitic insects, in that it consistently utilizes, for a period immediately after hatching, a carrier belonging to a different order from its probable host. The eggs are deposited in a cluster about a newly deposited *Selenothrips* egg, and hatching of the two is simultaneous. The planidia attach themselves to the young thrips as soon as they emerge from the eggs and maintain their position upon its body until the first molt. The particular advantage derived from this association is as yet undetermined.

Phoresy on the part of the first-instar larvae of parasitic insects is of general occurrence also in the coleopterous families Ripiphoridae and Meloidae and in the Strepsiptera. The larvae of these groups, as well as those of Hymenoptera of similar habit, are of the planidium type. Those of the above groups which require the services of a carrier are practically all parasitic upon or in the larvae of bees and nest-building wasps. The triungulinids are generally transported to the cell or nest by adult females of the host species.

IMMATURE STAGES

There is an exceptional variety in the size and form of the immature stages of the parasitic representatives of the order that has been made necessary by the different modes of reproduction and by the special conditions which must be met in order to permit successful parasitization and development. The latter requirements have brought about pronounced changes in various morphological characters, which are most evident in the egg and first-instar larva.

Richardson (1913), E. W. Wheeler (1923), and Imms (1925) have indicated the principal larval types known in the order, and H. L. Parker (1924) has presented a detailed study of the eggs and larvae of the Chalcidoidea and Cushman (1925*b*) of the main types of the Ichneumonidae. The grouping here given, in 5 egg types and 14 first-instar larval types, is a combination of these with certain revisions and additions made necessary by the more complete information now available on certain families. The most readily recognizable characters are considered to be predominantly adaptive, and these have been utilized in preference to the taxonomic characters, which are often microscopic and difficult to utilize except by experts in the particular groups. The characters used, because of their being adaptive, present many stages of development even within comparatively small groups, and intermediate forms often occur that possess modifications representing several groups. The line of demarcation between a number of the types is not well defined. In the intermediate forms, one character is usually more highly developed than others, and the larvae are assigned to the groups in which that character is dominant. Thus, caudate larvae bearing the anal vesicle are usually assigned to the caudate group, for the vesicle is less highly developed than in the true vesiculate type.

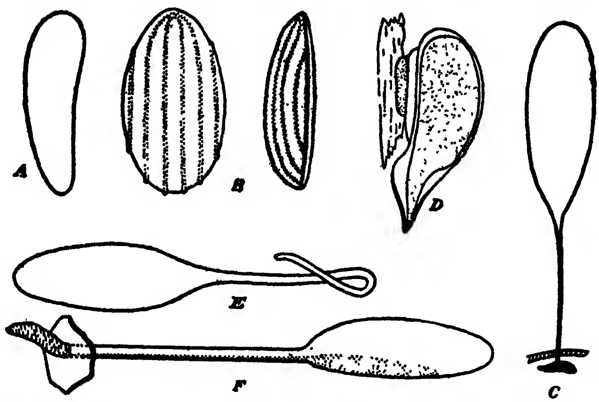


FIG. 2.—Egg types of the parasitic Hymenoptera. *A*, hymenopteriform; *B*, microtype; *C*, pedicellate; *D*, a form tentatively considered as modified pedicellate, with an "adhesive pad" on the ventral side; *E*, stalked; *F*, encyrtiform. Figures *A* to *D* with the anterior pole above; *E* and *F* with the stalk at the anterior end.

The various egg and larval types are briefly described herewith, and a statement is given as to the groups in which each occurs.

Egg Types. 1. *Hymenopteriform* (Fig. 2*A*).—Ovoid to spindle-shaped in outline, both ends smoothly rounded, and the chorion smooth or variously sculptured. Deposited internally, externally, or apart from the host. (Of general occurrence.)

2. *Microtype* (Fig. 2*B*).—Of minute size, oval in outline, flattened ventrally, and the chorion of the dorsum heavy, vitreous, and bearing longitudinal ridges.

Deposited apart from the host, and eaten by the latter before hatching. (Trigonalidae.)

3. *Stalked* (Fig. 2*E*).—A tube-like extension at one end, functionless after deposition, and often a "flagellum" at the opposite end. Deposited externally, internally, or apart from the host. (Of general occurrence in several superfamilies.)

4. *Encyrtiform* (Fig. 2*F*).—The anterior stalk and a portion of the egg body bearing a longitudinal rib, or aeroscopic plate, utilized by the larva in respiration. Deposited internally, with the tip of the stalk projecting from the oviposition puncture. (*Encyrtus*, *Microterys*, and many other Encyrtidae.)

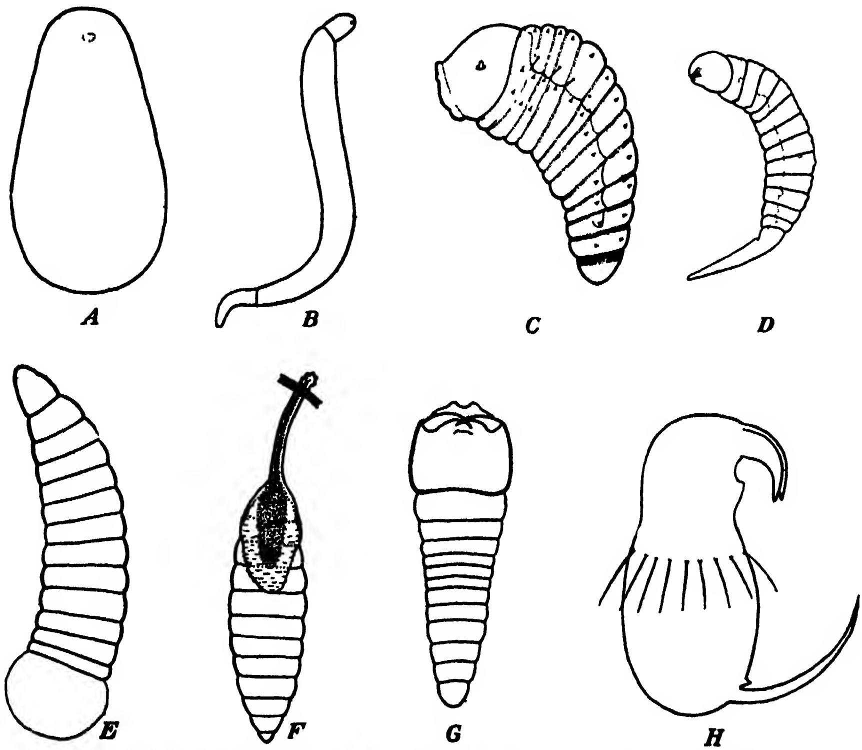


FIG. 3.—First-instar larval forms of the parasitic Hymenoptera. *A*, sacciform; *B*, asexual; *C*, hymenopteriform; *D*, caudate; *E*, vesiculate; *F*, encyrtiform; *G*, mandibulate; *H*, teleaform.

5. *Pedicellate* (Fig. 2*C*).—One end of the egg body variously modified to form an anchor, which is inserted in a puncture in the host integument, or the anterior end twisted or knotted into that form at deposition. External only. (Agriotypidae, many Tryphoninae and Lysiognathinae of the Ichneumonidae, several Eulophidae, and the male eggs of several species of *Coccophagus*.

First-instar Larval Types.—1. *Hymenopteriform* (Fig. 3*C*).—Body spherical to spindle-shaped, usually 12 or 13 visible body segments, the integument bare or with sensory setae and cuticular spines. Internal or external. (Of general occurrence.)

2. *Sacciform* (Fig. 3*A*).—Heretofore termed "embryonic." The body bag-like, without segmentation, and lacking the tracheal system. Internal only. (Some Dryinidae, Trichogrammatidae, and *Anagrus* of the Mymaridae.)

3. *Encyrtiform* (Fig. 3*F*).—Body of 10 or 11 distinct segments, with posterior spiracles only. The egg shell and stalk utilized for respiratory purposes. Internal only and hatching from the encyrtiform egg. (Many Encyrtidae.)

4. *Caudate* (Fig. 3*D*).—Distinctly segmented, the body usually somewhat elongate, and the last segment modified into a fleshy tail-like organ. Internal only. (Many Ichneumonoidea and Chalcidoidea, but rare in the Serphoidea.)

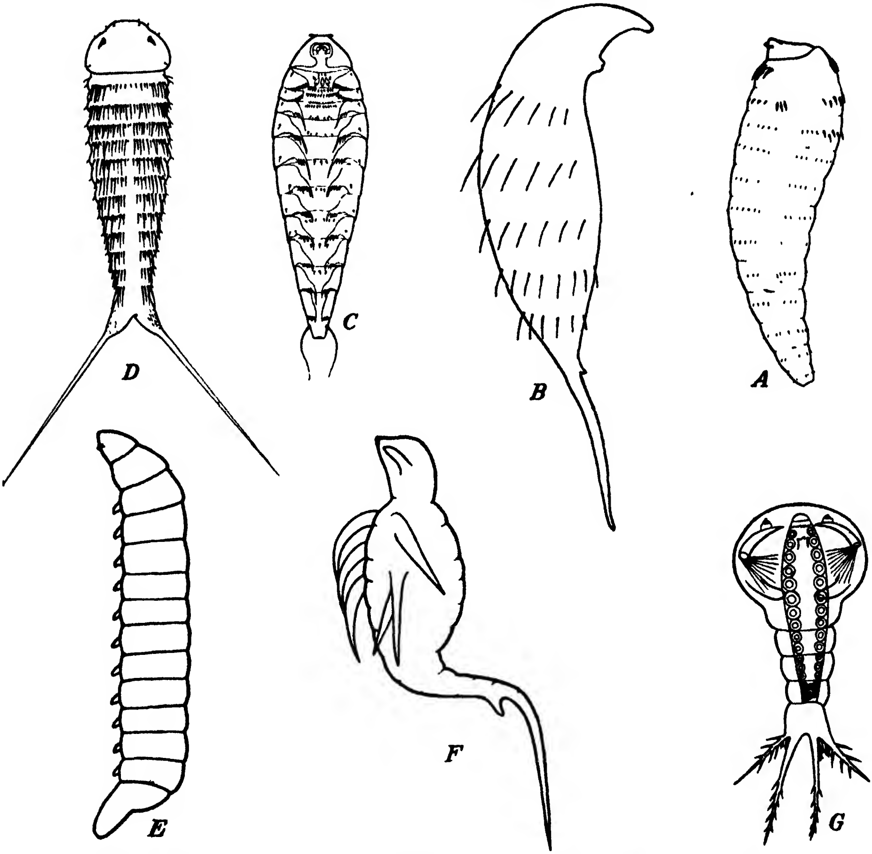


FIG. 4.—First-instar larval forms of the parasitic Hymenoptera. *A*, microtype; *B*, mymariform; *C*, planidium; *D*, agriotypiform; *E*, polypodeiform; *F*, eucoiliform; *G*, cyclopiform.

5. *Teleaform* (Fig. 3*H*).—Body segmentation not visible, but the cephalothorax and abdomen separated by a constriction; the mandibles very large, usually fleshy and directed ventrad; the abdomen almost spherical with one or more rings of long, delicate spines, and a long, heavily sclerotized blade-like process, directed ventrad, upon the last segment. Internal only. (Scelionidae.)

6. *Mymariform* (Fig. 4*B*).—The body spindle-shaped, with indistinct segmentation; the head produced in front into a conical process; the body segments with rings of long spines and the last segment prolonged into a tail-like organ. Internal only. (*Polynema*, *Anaphoidea*, etc., of the Mymaridae; *Poropoea* and *Ophioneurus* of the Trichogrammatidae.)

7. *Cyclopiform* (Fig. 4G).—Cephalothorax larger than abdomen; broader than deep, the mandibles very large, falcate, and lying transversely, the presumed first thoracic segment with a pair of fleshy processes ventrally; the abdomen narrow and tapering, with the last segment usually bifurcate, occasionally rounded. Internal only. (The majority of Platygasteridae.)

8. *Mandibulate* (Fig. 3G).—Segmentation distinct, the head very large, somewhat flattened, broader than long, heavily sclerotized, with the mandibles falcate and very large. Internal only. (Many Ichneumonidae, Braconidae, Serphidae, and Diapriidae.)

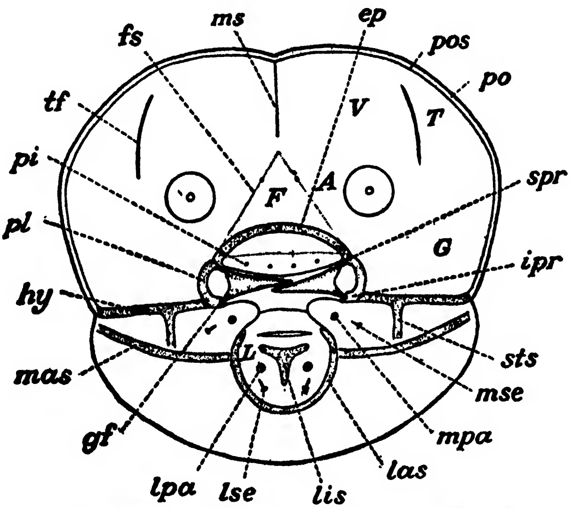


Fig. 5.—Front view, somewhat diagrammatic, of typical last-instar larval head of the parasitic Hymenoptera, showing the external characters. For names and descriptions of parts consult the original reference. (*From Vance and Smith*, 1933.)

9. *Agriotypiform* (Fig. 4D).—The body with a transverse row of long, heavy spines dorsally on each segment and the last abdominal segment bifurcate, the prongs being long, slender, sharply pointed, and heavily sclerotized. External only. (Agriotypidae. The larva of *Anastatus albitarsis* Ashm., though internal and having the rows of spines ventrally rather than dorsally, is placed in this group.)

10. *Vesiculate* (Fig. 3E).—Similar to the hymenopteriform except that the proctodeum is evaginated to form a somewhat spherical external vesicle. Internal only. (Many Braconidae, and of occasional occurrence in the Ichneumonidae and Encyrtidae.)

11. *Eucoiliform* (Fig. 4F).—The thoracic segments each bearing a pair of long fleshy processes ventrally, and the posterior segments of the abdomen tapering sharply, the last often produced into a fleshy tail-like organ. Internal only. (Eucoilinae of the Cynipoidea.)

12. *Polypodeiform* (Fig. 4E).—The body somewhat cylindrical, with the segments bearing paired fleshy processes of approximately equal length ventrally. Internal only. (Ibaliinae of the Cynipoidea, Serphidae, and Heloridae. Several Ichneumonidae show a tendency toward assumption of this form.)

13. *Planidium* (Fig. 4C).—Body fusiform, the segmental bands or plates heavily sclerotized, often with heavy spines, and the abdomen terminating in a suctorial or adhesive disk. External only at hatching. (All Eucharidae and parasitic Perilam-

pidae. The male larva of *Coccophagus gurneyi* Comp. approaches this type. For a further discussion of the planidium larva, see pages 17–19.)

14. *Microtype* (Fig. 4*A*).—Minute in size, with the integument delicate, and the thoracic segments each bearing heavy spines or hooks, some of which may be plate-like, dorsally and ventrally. Internal only, and hatching from the microtype egg. (All Trigonalidae.)

Intermediate- and Last-instar Larvae.—As has already been mentioned, the greatest variation in larval form occurs in the first instar and development thereafter tends toward a convergence to the hymenopteriform type. This may be complete

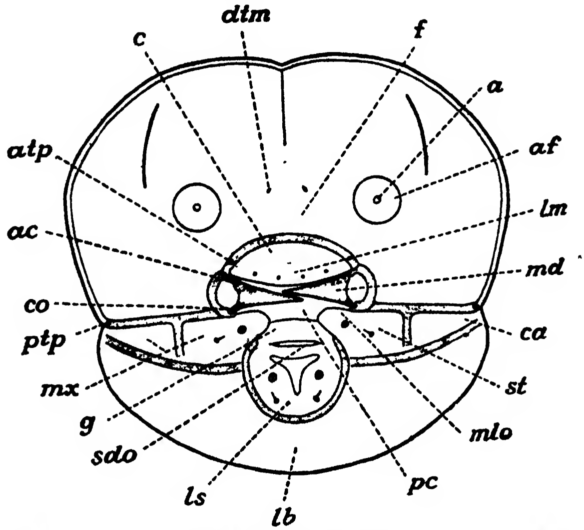


FIG. 6.—Additional external characters of the larval head of the parasitic Hymenoptera. (*From Vance and Smith*, 1933.)

in the second instar, or successive transitional forms may intervene between the first and the last instar. The greatest change at the first molt takes place among the species that have the most highly specialized first-instar larvae. In the planidium, cyclopiform, teleaform, agriotypiform, and mandibulate types of first-instar larva, the special morphological characters that distinguish them so readily are lost at the first molt, and the second-instar larvae are hymenopteriform or very close to that type. In certain of the Cynipoidea having eucoiliform first-instar larvae, the second instar is polypodeiform.

The encyrtiform larvae persist without essential change until the molt to the last instar, and they maintain their respiratory connection with the egg stalk until that time. In the caudate larvae, the tail is of reduced size in relation to the body after each molt and is lacking or rudimentary in the last instar. A corresponding reduction takes place in the fleshy ventral processes of the polypodeiform larvae in the few instances in which these structures persist beyond the first molt. An exceptional variation in larval form occurs in the different instars of the Trigonalidae. The trigonaliform first-instar larva is succeeded by an unspecialized form, and this in turn is followed by a distinctly mandibulate-type larva, which in other families of the order represents the first instar. The fourth and fifth instars are hymenopteriform.

Occasionally distinctive and readily recognizable larval forms appear in the intermediate or final instars. One of these is the so-called "histriobdellid" second-

instar larva of *Anagrus* which follows a sacciform first instar. The body is cylindrical, is divided into about six recognizable "segments," and bears a pair of large, curved, spine-like processes at the anterior end, which are apparently the mandibles, a pair of cylindrical or conical fleshy processes somewhat below the mandibles, and a pair of fleshy ear-like processes lateroventrally on the last "segment," or body division.

Another larval type, representing the last instar and quite different from the normal hymenopteriform larva, is that of the majority of Eucharidae; it reveals no segmentation except for constrictions between the three main body divisions and is entirely incapable of movement.

The presumed second and the last instar of the Agriotypidae are readily distinguished from others of the order by the presence of a pair of short but heavy opposed "hooks" at the caudal end of the body, but they do not depart otherwise from the normal form.

The morphological characters of the mature larvae of the order that are of particular value are found largely on the head, (Vance and Smith, 1933) and these are indicated in Figs. 5 and 6.

Planidium Larva.—The term "planidium" was first suggested by W. M. Wheeler to designate the first-instar larva of *Perilampus hyalinus* Say, discovered by H. S. Smith (1912). It is derived from the Greek and means "diminutive wanderer," a particularly appropriate appellation for the larvae of both the Perilampidae and the closely related Eucharidae, which Wheeler himself had studied. Thompson (1915*a*) has presented an extended study of this larval form, with particular reference to *Perilampus*.

The descriptive characters that distinguish the planidium larva are: (1) The fusiform body. (2) The uniform black, brown, or amber color of the entire body at the time of hatching. (3) The presence of heavily sclerotized segmental bands or plates extending over the dorsum and the lateroventral areas and terminating in pleural plates. The latter have not been recognized in the Perilampidae. In the newly hatched larvae, the segmental bands are overlapping, giving a telescopic effect. After feeding, the intersegmental membranes become greatly stretched, and the dark bands are widely separated and conspicuous against a white background. (4) The abdomen terminates in a sucker-like organ, and the last one or two segments bear a long pair of spines, or cerci, which may exceed the body in length. (5) The body is often of minute size in relation to the parent adult.

The characters of the planidium are adaptive and serve to meet the conditions that are encountered between the time of hatching and the establishment of contact with the primary or secondary host. Its small size is a result of the need of the species to deposit a very large number of eggs to compensate for the hazards involved during the first larval stage. The heavily sclerotized integument protects the larva from desiccation and injury and enables it to undergo a free-living period, without food, which extends in some species to one month or longer. The caudal sucker and the long cerci enable it to stand erect when awaiting the approach of a host and to jump considerable distances. These habits are of importance where contact needs to be made with an active host or with an insect carrier for transportation to the host nest or cell.

The term planidium was originally given only to the larvae of the Perilampidae and Eucharidae, but it has since come to have a wider application, which may well be even further extended. In reviewing the parasitic and predaceous first-instar larvae of the different orders, one is impressed with frequent recurrence of this type of larva. It is a striking illustration of convergence in evolution, wherein a common form has developed in several orders to meet the same conditions. The orders and lower groups that may be considered in this connection are as follows:

Hymenoptera:
- Perilampidae (all parasitic species).
- Eucharidae (all species).

Diptera:
- Cyrtidae (all known species).
- Tachinidae (*Gymnocheta, Euphasiopteryx, Ormiophasia,* etc.).
- Sarcophagidae (*Parafeburia, Cirillia,* etc.).

Strepsiptera (all species).

Coleoptera:
- Ripiphoridae (all species).
- Meloidae (*Tricrania,* etc.).

All these have first-instar larvae with the characters already described. In addition, the following habits, many of which are peculiar to species having this type of larva, are found in all the groups listed above:

1. The eggs are deposited entirely apart from the host.
2. The larvae are able to pass an extended free-living period without food.
3. The larvae are able to stand erect, and many are capable of jumping.
4. The larvae are strongly attracted to any moving object and thus attach themselves to the host or to an essential carrier.

In addition to the groups enumerated above, there are several others that show a distinct trend toward the assumption of the planidium type of larva. Even in the Aphelinidae, of the chalcidoid Hymenoptera, it has been found that the male larva of *Coccophagus gurneyi* Comp. possesses the segmental plates and other characters of the planidium. In contrast to the simple larva of the female, which lies in the body cavity of the host, it must pass through an extended waiting period in the drying remains of the secondary coccid host before the primary host is in a suitable stage for attack.

Among the Diptera, the Nemestrinidae, Bombyliidae, certain other Tachinidae (*Archytas, Eupeleteria, Bonnetia, Linnaemyia, Prosena,* etc.) and Sarcophagidae likewise have free-living larvae which are becoming specialized and assuming the planidium form. Various transitional forms are known in the Tachinidae.

The first-instar larva of *Tricrania* is more distinctly of the planidium type than are those of other genera of Meloidae. They all possess, however, the essential characters and habits of the planidium, but the term "triungulinid" is retained, because of long usage, to designate the larvae of this family as well as those of the Ripiphoridae and Strepsiptera.

TENTHREDINOIDEA

TENTHREDINIDAE

The adults of a number of species of the family have developed the predaceous habit and subsist, in part at least, upon other insects. K. Iwata has found that those of *Tenthredella nigropicta* Smith feed extensively upon the larvae and pupae of chrysomelid beetles of the genera *Melasoma* and *Plagiodera* in Japan and that two or three full-grown larvae are eaten each day. Hobby (1932) has listed the different species and their prey recorded in England. These include *Tenthredo, Tenthredella,* and *Rhogogaster,* and their prey comprises chiefly the small Diptera and some Hymenoptera (sawflies only). The flies that frequent flowers

appear to be favored, possibly because of ease of capture during feeding. Species of the genera *Macrophya*, *Tenthredopsis*, and *Taxonus* have also been noted to have the predaceous habit. In practically all instances, the predatory individuals are females.

ORYSSIDAE

The genus *Oryssus*, upon which the family is based, comprises only a very few species. While suspected of being parasitic in habit it was not until 1917 that H. E. Burke definitely established that *O. hopkinsi* Roh. and *O. occidentalis* Cress. were solitary internal parasites of the larvae of buprestid beetles. Practically nothing further is known regarding the habits of these species, and of the immature forms only the last-instar larva and the pupa have been described.

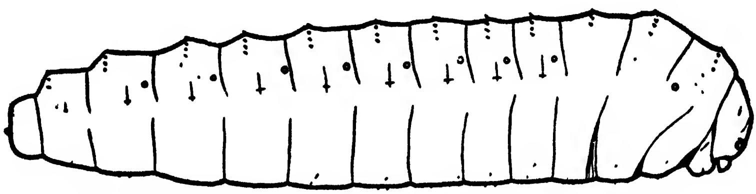


FIG. 7.—The mature (?) larva of *Oryssus occidentalis* Cress. (*From Parker*, 1934.)

The mature larva of *O. occidentalis* (Fig. 7) (Rohwer and Cushman, 1917; H. L. Parker, 1934) bears a considerable resemblance to a chalcidoid larva of the same instar. It is subcylindrical, with 13 body segments, the legs indicated by sclerotized disks, and each segment bears a transverse row of four or five short, stout spines at each side of the dorsal median line. There are 10 pairs of spiracles, situated on the last two thoracic and the first eight abdominal segments. Those of the metathorax, which Parker does not figure, are rudimentary and nonfunctional. The head is small, with tubercle-like antennae, and the mandibles narrow and tridentate.

The pupa of the female bears the ovipositor over the dorsum, and it extends forward slightly beyond the head. The second to eighth abdominal tergites bear transverse rows of spines at the sides.

ICHNEUMONOIDEA

The superfamily Ichneumonoidea constitutes one of the largest groups of parasitic insects; and, from the point of view of effectiveness in reducing or holding in check the numerous pests that infest plants, it probably takes first rank, excelling even the Tachinidae. The dominant families are the Ichneumonidae and Braconidae, and species of one or both families are found to attack the great majority of plant pests.

BRACONIDAE

This family is one of the major groups of insect parasites and includes a great number of species that are sufficiently effective to exert a very definite check upon the increase of numerous important plant pests. The hyperparasitic habit is much less developed than in the Ichneumonidae—in fact its occurrence is rare—and the family is consequently almost wholly beneficial. The principal exceptions are the species of *Perilitus* that parasitize the adults of the entomophagous Coccinellidae.

Several species of Braconidae have been of considerable value in the biological control of insect pests. *Ischiogonus syagrii* Ful. was imported into Hawaii from Australia in 1921 for use against the fern weevil, *Syagris fulvitarsis* Pasc., and is credited with controlling it. *Opius fletcheri* Silv., a parasite of the melon fly, *Bactrocera curcurbitae* Coq., and *O. tryoni* Cam., which attacks the Mediterranean fruit fly, *Ceratitis capitata* Wied., have appreciably reduced the infestation of these two pests in Hawaii and have thus permitted the growing of certain fruits and vegetables that previously were too heavily infested for profitable commercial production. The reduction in infestation of the latter pest in coffee has been particularly striking. *Apanteles solitarius* Ratz. and *Meteorus versicolor* Wesm., both of European origin, have been responsible for adequate control of the satin moth, *Stilpnotia salicis* L., in several sections of North America.

HOST PREFERENCES

Because of the large number of species involved and the extensive studies that have been made upon many of them, the host preferences will be discussed on the basis of the principal subfamilies. There is an exceptional uniformity of habit within these groups, not only in the choice of hosts but in the manner of development.

The Vipioninae are predominantly external parasites of the larvae of Lepidoptera, though a considerable number attack coleopterous larvae and a few species are parasitic upon those of sawflies and Diptera (Cecidomyiidae). The dominant genus is *Microbracon*, which is cosmopolitan and attacks a wide range of hosts. Practically all hosts attacked by members of this subfamily are contained in a cell, burrow, or cocoon or are protected by a web. Free-living larvae normally are not subject to attack, though an undetermined species of *Microbracon* observed by Beeson and Chatterjee (1935) parasitizes the uncovered larvae of the teak leaf skeletonizer, *Hapalia machaeralis* Wlk., in India and *M. brevicornis* Wesm. attacks the free-living larvae of *Heliothis* in South Africa. Most species are gregarious in habit, though the number developing on

each individual host is not great. An occasional species is predaceous rather than parasitic, such as *M. lendicivorus* Cush., discussed by Williams (1928), which develops at the expense of the larvae of the cecidomyiid, *Asphotrophia fici* Barnes. These larvae live in the receptacles of the fruit of *Ficus nota* in the Philippine Islands.

Relatively few studies have been made upon the Spathiinae and Doryctinae, but the species appear to attack principally the larvae of bark and wood-boring Coleoptera. The genera most commonly encountered are *Spathius*, *Doryctes*, and *Dendrosoter*, which are externally parasitic in habit.

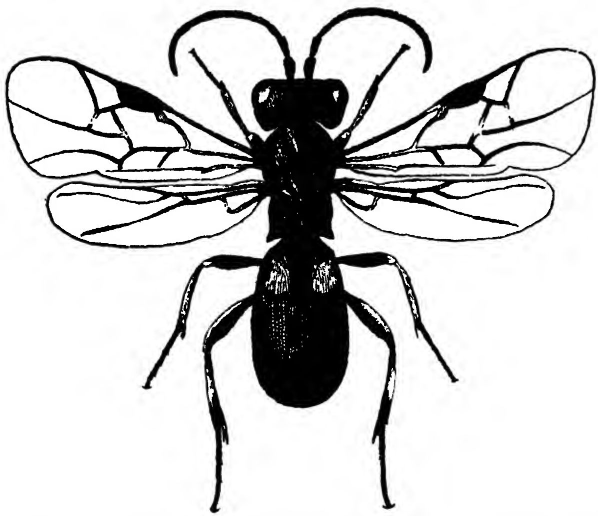


FIG. 8.—The adult female of *Chelonus annulipes* Wesm. (*From Vance*, 1937.)

The Rhogadinae, so far as known, are limited in their host preferences mainly to the larvae of Lepidoptera, upon which they develop internally. *Rogas* is the most commonly encountered genus of the subfamily. *Oncophanes lanceolator* Nees differs in habit from others of the subfamily in developing as a gregarious external parasite.

The Cheloninae are predominantly solitary internal parasites of lepidopterous larvae. The genera *Ascogaster*, represented by the well-known *A. quadridentata* Wesm. (*carpocapsae* Vier.), *Phanerotoma*, and *Chelonus*, are restricted to lepidopterous hosts and have the habit of ovipositing in the egg and completing their larval development when the host larva is nearly mature.

The Triaspinae are parasitic in the larvae of Bruchidae and occasionally Curculionidae, but very little information is available regarding the manner of attack and development. *Triaspis* is a well-known genus frequently reared from weevil-infested beans, peas, and other seeds.

Very little information is available regarding the host preferences of the Neoneurinae. *Elasmosoma berolinense* Ruthe is recorded by Kariya (1932) as attacking adult ants of *Formica fusca* var. *japonica* Motsch. It is stated that the female pounces upon the ants at the entrance to the nest and inserts the ovipositor into the abdominal region. Observations on American and European species point also toward a relationship with ants.

The Microgasterinae are limited in their host preferences mainly to lepidopterous larvae, and many of the hosts are free-living in habit. The dominant genera are *Apanteles*, *Microgaster*, and *Microplitis*, and these are of very common occurrence. Development takes place internally, the only apparent exception being *A. canarsiae* Ashm., which is recorded and figured by Strauss (1916) as a solitary external parasite of the larva of *Desmia funeralis* Hbn. This record, however, must be regarded as questionable, for it may be based upon observations made during the very short period of external feeding which occurs in some species between emergence from the host body and spinning of the cocoon.

The Braconinae are most frequently found as parasites of lepidopterous caterpillars, though a number of species attack trypetid and curculionid larvae. The species of the well-known genus *Bassus* develop internally in lepidopterous larvae of shoot- or stem-boring habit.

Relatively little is known regarding the host preferences of the Blacinae. *Eubadizon* and *Orgilus* are parasitic in lepidopterous larvae, whereas *Syrrhizus* attacks adult chrysomelid beetles of the genus *Diabrotica*.

The Macrocentrinae are solitary or gregarious internal parasites of lepidopterous larvae. The dominant genus *Macrocentrus* is well-known through the studies made on several species that attack the European corn borer and the oriental fruit moth. Initial attack is upon the young larva in its burrow, and the development of the parasite is completed when the host larva is full-grown.

Information regarding the subfamily Opiinae relates principally to the genus *Opius*, many of which are parasitic in dipterous larvae of the family Trypetidae, though a number of species have been reared from Agromyzidae. Oviposition takes place in the maggot in almost any stage of development, and adult emergence is from the host puparium.

The Euphorinae are of distinctive habit in that the great majority of species are internal parasites of adult Coleoptera. The well-known genus *Perilitus* (*Dinocampus*) is confined in its host preferences to Coccinellidae and Curculionidae, whereas *Microctonus* attacks mainly the Curculionidae, Chrysomelidae, and Tenebrionidae. *Perilitus* is solitary in habit, but in some species of *Microctonus* a large number may develop

in a single host. *Aridelus* attacks nymphs and adults of Pentatomidae, and *Euphorus* and *Euphoriana* are parasitic in Miridae (Muesebeck, 1936). There are several exceptions to the above generalization regarding the host stage attacked. *M. aethiops* Nees has been reared from adults and larvae of *Phyllotreta* and *Sitona*, and *M. brevicollis* Hal. has its first generation in the larvae of *Haltica ampelophaga* Guer. and the second in the adult beetles (Kunckel D'Herculais, and Langlois, 1891).

The Meteorinae are solitary or gregarious internal parasites of the larvae of many Lepidoptera and have also been recorded from those of bark and wood-boring Coleoptera. Extensive studies have been made

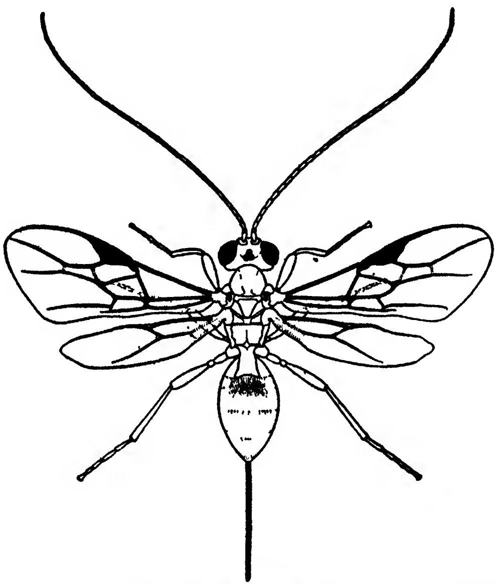


FIG. 9.—The adult female of *Opius fletcheri* Silv. (*From Willard*, 1920.)

on the habits of a number of species of *Meteorus*, the single genus of the subfamily. Oviposition takes place in the young host larvae while they are exposed, and development is completed before the pupal stage is attained. Some species produce two complete generations upon one brood of host larvae, the first being upon very young individuals and the second upon those which are nearly mature.

The Aphidiinae are exceptionally consistent in their host preferences, and all species that have been studied are solitary internal parasites of Aphididae. They are often very effective in checking infestations of their hosts, though this usually takes place after the latter have reached a high population level and considerable injury to the crop has already occurred. This is due to the ability of the aphids to reproduce at lower temperatures than do the parasites, and the pest population is conse-

quently built up to a relatively high level before conditions for parasite development become favorable. The more common genera are *Aphidius*, *Lysiphlebus*, *Praon*, and *Ephedrus*.

The Alysiinae have not been extensively studied, but the more common members of the subfamily, of the genera *Alysia* and *Dacnusa*, are internal parasites of Diptera. *Alysia* is more particularly a parasite of blowflies of the genera *Sarcophaga*, *Lucilia*, and *Calliphora*, and the adult emerges from the puparium. Extended studies of *A. manducator* Panz., have been made by Graham-Smith (1916, '19), Altson (1920), Myers (1927*a*), Salt (1932), and Holdaway and Smith (1932). Several species of *Dacnusa* likewise attack the larvae and emerge from the puparia, the principal hosts being of the family Agromyzidae.

Cushman (1926*a*) has pointed out the influence that the position of the host larvae with respect to the plant may have upon parasite attack. A given parasite species may attack two or more hosts that are widely separated taxonomically but have the same relationship to the plant, whereas closely related species, but of different habit, are not subject to attack. He concludes that the relationship of the host insects to the plant, rather than taxonomic relationships, often governs the choice of hosts by the parasite. This applies not only to many Braconidae but to various other parasitic groups, and even to some predators.

Several earlier authors have pointed out the close association of parasite species with a particular plant species or group, which necessarily limits their attack to insects infesting those plants. Picard (1919), in his studies on the insects associated with fig trees, came to the conclusion that *Sycosoter lavagnei* P. & L. is primarily attracted to this tree rather than to the particular coleopterous species which it parasitizes. Taylor (1932) states that in South Africa *Microbracon brevicornis* attacks larvae of *Heliothis armigera* Hbn. on *Anthirrhinum* only, even though caterpillars are present on many other plants.

The food plant upon which the host develops often has a pronounced influence upon the extent of parasitization. This is strikingly shown in the case of *Apanteles congregatus* Say, a common parasite of *Phlegothontius* larvae in North America. When these are feeding upon wild Solanaceae, the parasitization is often heavy. Morgan (1910) points out, however, that larvae occurring upon tobacco are very seldom parasitized, and he believes that parasitized individuals found upon it may have crawled to that plant from native vegetation. This difference in degree of successful attack is thought to be due possibly to the toxic effect of the food of the caterpillar upon the early stages of the parasite.

Further observations upon *Apanteles* parasitization of *Phlegothontius* have been made by Gilmore (1938), who finds that the lack of effective parasitization is most pronounced when the host occurs upon dark-fired

tobacco. It was found that larvae feeding solely upon such foliage were frequently parasitized but that the *Apanteles* larvae were unable to develop to maturity. The nicotine content of this type of tobacco is very high, and it is suggested that this toxic principle may be present in sufficient concentration in the blood of the host to bring about the death of the parasitic larvae.

BIOLOGY AND HABITS

Parasitism by Braconidae may be either internal or external, and modifications in habit in this respect are correlated with the habits of the host stages that are subject to attack. In general, internal parasitism occurs if the hosts are free-living, as illustrated by the adult beetles attacked by the Euphorinae and other groups, the foliage-feeding

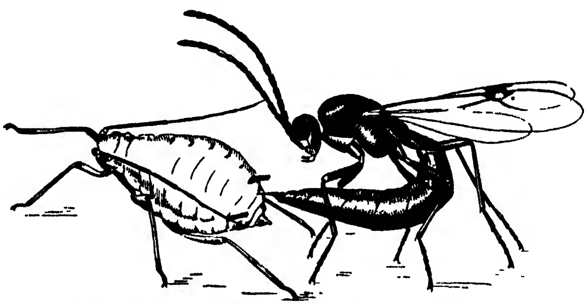


FIG. 10.—A female of *Lysiphlebus testaceipes* Cress. ovipositing in an aphid. (*From Webster*, 1909.)

lepidopterous larvae parasitized by Microgasterinae, Meteorinae, etc., and the aphids that serve as hosts of the Aphidiinae. External parasitism, on the other hand, is general in hosts that live in confined quarters and consequently the Vipioninae, which attack principally caterpillars in tunnels, leaf rolls, etc., and the groups that occur upon the larvae of bark and wood-boring Coleoptera, develop in this way. The latter groups complete their development upon the host instar upon which the egg is deposited.

The Cheloninae, Triaspinae, and Macrocentrinae are apparent exceptions to the above generalization, for they are internal parasites of hosts occurring in burrows or cavities in plant stems, fruits, and seeds. These species, however, oviposit either in the egg or the young larva but attain larval maturity in the fully grown host, so that the internal habit is essential.

Habits of the Adult.—The adults of the great majority of species doubtless feed principally upon honeydew and various plant exudations; but the females of a considerable number subsist largely, if not entirely,

upon the body fluids of the host stages that they attack. This latter habit occurs most generally in the subfamily Vipioninae and occasionally in the Microgasterinae also. It is particularly well-developed in the genus *Microbracon* and has been noted in practically all species that have been studied. The host-feeding habit was first observed by Trouvelot (1921) in *M. gelechiae* Ashm. (*johannseni* Vier.); and this author, and Genieys (1925) in the case of *M. brevicornis* Wesm., have described the habit in some detail and given an account of the formation of the feeding tube under the conditions that prevent normal direct feeding. The latter author states that ordinary laboratory food materials do not fulfill the nutritional requirements of the parasite female and that feeding on the body fluids of the host larva is essential before oviposition can take place. *Chelonus shoshoeanorum* Vier., is said to feed on the fluids that exude from the puncture in the egg of the host.

A considerable number of species are able to begin oviposition on the day of emergence of the female from the cocoon, though there is no uniformity in this respect even within genera. *Opius fulvicornis* Thoms. is ready for immediate oviposition, whereas *O. melleus* Gahan requires a gestation period of about 13 days. *Apanteles melanoscelus* Ratz. (Crossman, 1922) and *Ascogaster quadridentata* are ready for oviposition very soon after emergence. *Microbracon* apparently requires as much as 15 days, depending upon the species. Genieys has noted an unusual condition in *M. brevicornis*, in which unmated females begin oviposition 4 to 5 days after emergence, whereas those which are mated require an interval of 14 to 18 days. Several authors have given the gestation period as the time elapsing between mating and first oviposition but, with the exception of the above instance, this has no bearing upon the time at which the first eggs are laid, as oogenesis proceeds irrespective of whether or not mating has taken place. In his extended studies upon the biology and habits of *M. hebetor* (as *M. brevicornis*), Hase (1922) found that females can be successfully mated and produce female progeny even after a period of 40 days, during which time male progeny are produced at the normal rate. Oviposition is inhibited at temperatures below 15°C.

The external parasites among the Braconidae usually attack host larvae that are half-grown or larger and that are contained in cells, leaf rolls, or burrows or are beneath a web or other covering. The females of some species of *Microbracon* penetrate the burrows of the host and attack the larvae directly. *Bracon glaphyrus* Mshll. burrows in the soil in search of *Baris* larvae, and *Bracon* sp., probably *hylobii*, scrapes away the frass at the entrance of the burrow of *Hylobius*, turns about, and inserts the ovipositor into the burrow. The female of *Cardiochiles nigriceps* Vier. straddles the young host larva and inserts the ovipositor

by a downward thrust, whereas most other species of internal parasites oviposit by a forward thrust of the ovipositor between the legs. In *Apanteles*, several earlier authors have insisted that oviposition is in the host egg, but this has not been proved in any instance. *A. militaris* Walsh inserts the ovipositor in the body of the caterpillar and then folds its legs and retains its hold only by the ovipositor. *A. glomeratus* L. oviposits by preference in the newly hatched cabbage worms (Picard, 1922). In attack by *A. machaeralis* Wlkn. upon young caterpillars of *Hapalia*, the latter drop from the leaves and suspend themselves by a silken thread, whereupon the parasite quickly descends the thread and accomplishes oviposition. *Meteorus hypophloei* Cush. will attack bark-beetle larvae only when they are crawling about on the surface of the bark. Among the Euphorinae, the species of *Perilitus* normally effect oviposition in the host beetles by inserting the ovipositor through the intersegmental membrane in the abdominal region. Several authors have stated that *P. coccinellae* oviposits in larvae and pupae as well as in the adult beetles, but this has not been substantiated. *Microctonus melanopus* Ruthe is stated by Speyer (1925) to insert the ovipositor through the anal opening of the host or the membrane near by. The female of *Euphorus helopeltidis* Ferr. jumps upon the back of the mirid nymph, curves the abdomen beneath the body, and makes the insertion in an abdominal suture or at the base of a coxa (Menzel, 1926, '29). The females of *Syrrhizus diabroticae* Gahan, which oviposit in adult *Diabrotica* beetles, mount upon the back of the host, and the ovipositor is inserted dorsally at the base of the elytra. *Cosmophorus henscheli* Ruschka has a quite different habit; the female attacks the host beetle head to head, grasps the back of the thorax between the mandibles, and then brings the ovipositor forward and inserts it in one of the thoracic sutures.

Among the species that are endoparasitic and gregarious, the full complement of eggs is usually deposited at one insertion of the ovipositor, and often very quickly. Thus, the female of *Apanteles militaris* deposits up to 72 eggs at one insertion, and the time required does not exceed one second (Tower, 1915). A different procedure is apparently followed by *A. sagax* Wlkn., which develops in considerable numbers in the caterpillars of *Sylepta derogata* F. According to Wilkinson (1937), the eggs are deposited singly and at some distance from each other.

Host larvae attacked by Braconidae of endophagous habit are usually permanently and completely paralyzed. An exception to this is *Microbracon pini* Mues., which inflicts only temporary paralysis, lasting about one hour, upon the larva of *Pissodes strobi* Peck. The *Bracon* sp. recorded by Munro (1917) as attacking the larvae of *Hylobius abietis* L. does not sting the host. The hosts of these parasites are contained in burrows

and move very little during the course of normal feeding, so that there is little danger of loss of the parasite egg or larva.

Donohoe (unpublished notes) has found that some of the larvae of *Ephestia figulilella* Greg. which have been stung by *M. hebetor* Say are able to effect complete recovery. In the first 15 days of parasite activity, 12 per cent of the hosts recovered, while 29 per cent of those attacked during the third 15-day period recovered, showing a progressive lessening in effectiveness of the sting.

The internal parasites seldom even temporarily paralyze their hosts, though larvae of bark beetles attacked by *Coeloides dendroctoni* Cush. become inactive and appear paralyzed within two days after attack and are dead on the third day (De Leon, 1935*b*). The larval hosts of *C. pissodis* are permanently paralyzed and sometimes killed by the sting. The adult scolytid beetles attacked by *Cosmophorus henscheli* are paralyzed for one hour or more but recover completely. Dipterous larvae parasitized by *Alysia manducator* are paralyzed for a period of one to two minutes, and recovery is accompanied by pronounced writhing movements. Repetition of attack upon the same individual results in its death in one or two days, evidently from an excess of poison.

Among the groups that oviposit in the host egg, such as *Ascogaster*, *Chelonus*, and *Phanerotoma*, the stage of development of the egg at the time of parasite oviposition has an appreciable influence on the extent to which attack is successful. In *A. quadridentata* (*carpocapsae* Vier.), it has been found by Cox (1932) that the female will oviposit in codling-moth eggs in any stage of development, though parasitization is not successful if the "black-spot" stage has been attained. Rosenberg (1934) secured successful parasitization even in that stage. The egg is placed more or less at random in the cytoplasm, but in such a position that it is always outside the host embryo when the latter becomes fully formed. Entry into the body of the host embryo is accomplished by the newly hatched larva. Vance (1932*b*) has determined that females of *C. annulipes* Wesm. oviposit indiscriminately in corn-borer eggs of any stage of development, but Wishart and Van Steenburgh (1934) have shown that there is a marked difference in the number which attain maturity when oviposition takes place in those of different ages. Maturity was reached by 26.6 per cent of the parasite individuals when the host eggs were less than 24 hours old, 36 per cent in those which were two and one-half days old, and only 11.4 per cent in those which were nearly ready to hatch. In fresh eggs, there is a considerable chance that the larva will be found outside the body of the embryo after it has developed, in which case no further growth can take place. It may, however, pass between the lateral folds before completion of the dorsal closure and become successfully established. Eggs placed in

the yolk after dorsal closure are a complete loss. After rotation of the embryo has taken place, practically all eggs are placed within it.

Among the Microgasterinae the only species known to oviposit in the host egg is *Microgaster marginatus* Nees, which is a parasite of *Polia* spp. in Russia (Zorin, 1930). The egg is deposited in the host embryo during the 24 hours preceding hatching.

Among the Alysiinae are several parasites of Diptera which oviposit in the host egg but do not attain larval maturity until the pupal stage is reached. Examples of this habit are *Sympha agromyzae* Roh. in *Agromyza, Coelinidea meromyzae* Forbes in *Meromyza*, and *C. niger* Nees in *Chlorops*.

The only instance of maternal care of the immature progeny by Braconidae is *Cedria paradoxa* Wlkn., which is a gregarious external parasite of the larvae of *Hapalia machaeralis* Wlk. and other Pyralidae in India (Beeson and Chatterjee, 1935) and of *Margaronia pyloalis* Wlk. in China (Chu, 1935). These authors emphasize the persistence of the female with the brood after the host has been stung and the eggs laid, and this care continues until the progeny attain the adult stage. Another host may then be attacked, and the same course of events takes place. Chu states that the females do not feed during this period. A maximum of five broods is produced by each female, and the number of individuals in each brood decreases progressively. The averages for a series of females producing four broods was found to be 31.4, 20.3, 11.0, and 3.0 eggs in successive ovipositions. The first-named authors conclude, however, that the total number of eggs deposited upon a series of hosts is no greater than may normally be laid upon a single one, and imply that a female normally attacks only one host individual during her lifetime. They consider that the chief purpose of the care of the brood is to protect it from attack by chalcidoid parasites.

Development of the Immature Stages.—Following the deposition of the egg, an increase in size occurs during incubation in the great majority of species that develop within the host body. This is due to the absorption of host fluids by the developing embryo. This enlargement often causes the egg to become nearly spherical in form, and the caudal pedicel may largely or entirely disappear because of the stretching of the chorion. In *Apanteles thompsoni* Lyle (Vance, 1931), the increase is about three times in width and eight times in length. The greatest increase in size during incubation apparently occurs in the Euphorinae and Meteorinae. Ogloblin (1913) states that the egg of *Perilitus coccinellae* Schr. increases from 0.08 by 0.02 to 0.4 by 0.2 mm., amounting consequently to about 1,000 times by volume. In *P. rutilus* Nees (Jackson, 1928), the growth is approximately 1,200 times by volume. Balduf (1926*b*) mentions the appreciable difference in size of eggs of *P. coccinellae* while still within

the ovaries of the female, some being 0.08 mm. in length whereas others measure up to 0.29 mm. This is considered to be due to the retention of the latter individuals for a longer period in the oviduct and possibly to absorption of fluids from the parent. The extreme in egg growth during incubation is recorded by Strickland (1923) in *Meteorus dimidiatus* Cress., a parasite of cutworm larvae in North America. At the time of deposition the egg measures 0.14 by 0.04 mm. whereas just prior to hatching it is practically spherical, with the pedicel barely showing, and ranges up to 1.5 mm. in diameter. This growth takes place very rapidly and dimensions of 0.28 by 0.12 mm. were noted within 30 minutes after deposition of the egg.

The eggs of the ectophagous species are usually lightly adherent to the integument of the host, though some are placed only in the immediate vicinity of the host, whereas in the endophagous species they are free-floating or lodged among the muscles. Faure (1926) states that the eggs of *Apanteles glomeratus* are attached by their pedicels to the internal organs of the host caterpillar, but other authors do not corroborate this observation. In *Opius fletcheri* (Willard, 1920), they are said to be firmly attached at one end to the inner wall of the integument of the host by a mass of dark material which may represent a clot formed at the wound.

Little need be said regarding the larval habits of the Braconidae, for they differ only in relatively minor respects from those of other groups. Of particular interest, however, is the early larval development of *Ascogaster*, the first instar of which is under the necessity of penetrating the host embryo after spending 10 to 14 hours in the cytoplasm surrounding it; this is in contrast to the habit of *Chelonus*, which places the egg directly within the embryo or in such a position in the cytoplasm that it is enveloped by the growing germ band. The *Ascogaster* larva is minute at hatching, being only 0.2 mm. in length, but increases to 10 times that length and 250 times in volume before the first molt (Rosenberg, 1934). The anal vesicle constitutes one-sixth of this volume.

In *C. annulipes*, the development of the larva within the body of its host is appreciably affected and controlled by the physiological condition of the latter (Bradley and Arbuthnot, 1938). This is illustrated by a series of rearings upon single- and multiple-brooded strains of the European corn borer at 26.7°C. and 70 per cent relative humidity. In the former, all larvae remained in the first stage for 20 to 36 days, no second-instar larvae appeared before the twentieth day, and no third-instar larvae before the twenty-fourth day. In contrast to this, development in the multiple-brooded strain progresses much more rapidly. In no case did the first larval stage extend beyond 15 days, the second stage 17 days, or the third stage 19 days after oviposition.

No species of the family is known to retain a connection with the egg shell after hatching, and the larval exuviae are usually entirely discarded by the succeeding instars. In *Macrocentrus abdominalis* F., however, the second-instar larva retains the first exuviae in ribbon-like form at the posterior end of the body, and some species of *Apanteles* retain it as a band about the abdomen immediately in front of the anal vesicle (Fig. 17*C*).

The species of Opiinae and Alysiinae that attack dipterous larvae, but emerge from the puparia, quite consistently delay the first larval molt until pupation of the host, or at least until the puparium is formed, after which development is very rapid, and the perfect pupal stage is usually not attained by the host.

In the gregarious species of Microgasterinae, the emergence of the brood of larvae from a host caterpillar takes place almost simultaneously. Gatenby, in referring to *Apanteles glomeratus*, concludes that the outward

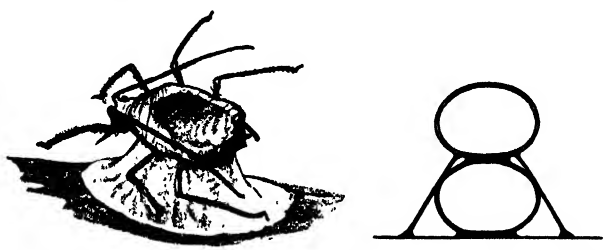


FIG. 11.—A dead parasitized aphid with the cocoon of *Praon simulans* Prov. beneath (*from Howard*, 1891) and, at right, a diagrammatic sketch showing the outer and inner cocoons of the parasite beneath the host body (*from Wheeler*, 1923).

movement of the more advanced individuals is due to a physiological stimulus and that their movements influence the remainder to do likewise. In this subfamily, the third instar is usually external and nonfeeding, the second molt being coincident with emergence from the host, and the anal vesicle is retracted at emergence or immediately thereafter. In *A. militaris*, its retraction takes place late in the second instar, whereas in *A. sesamiae* Cam. (Ullyett, 1935) the vesicle is stated to persist throughout the third stage. Third-instar larvae of *A. lacteicolor* Vier. have been found still within the host body, and they apparently do some feeding. In those species which form the cocoon on the body of the host, the anal vesicle often remains embedded in the wound until the preliminary phases of cocoon formation are completed. Many species leave exuviae in the wound at emergence, and this explains, at least in part, the lack of bleeding from the relatively large perforations in the body wall.

In the gregarious species of *Macrocentrus*, the larvae, while within the host, are all oriented with the head toward that of the host, but during the following period of external feeding they lie in the opposite

direction. After spinning of the cocoon, there is still another reversal of position, so that the pupae are always oriented in the same way as the host. The third larval molt takes place at the time of emergence from the host body.

The mature larva of *Perilitus*, after completing its feeding in the body of the beetle host, accomplishes emergence by cutting a hole through the thin membrane between two segments of the abdomen, usually near the posterior end of the body. *P. coccinellae* does so dorsally between the fifth and sixth abdominal segments. In some instances, it has been reported that emergence is through the anal opening, but it was more probably through an incision in the membrane near by. In the species of the family, such as *Syrrhizus*, that kill the adult host prior to emergence of the larvae, the point of exit is between the abdomen and thorax, or head and thorax, rather than at the posterior end of the body.

The persistence of the embryonic membrane, or trophamnion, as an envelope partly or completely enclosing the first-instar larva has been noted in a large number of species of Braconidae, particularly among the Microgasterinae, Meteorinae, Euphorinae, and Opiinae. Tower states that the larva of *Apanteles militaris* is still enclosed in the membrane after escape from the egg and that it soon cuts through the membrane in the mouth region and begins feeding. As growth proceeds, the membrane is further disrupted and falls away, though portions of it may remain about the body until the first molt. In *A. thompsoni*, according to Vance, the same situation exists, and several weeks elapse before the larva frees itself completely from the membrane. Gatenby (1919) has noted that the membrane of *Microgaster connexus* persists until the larva is approximately 2.5 mm. in length, indicating that a considerable period is passed within it, and very appreciable growth takes place due to the food derived from it. This is the case also in *Dacnusa areolaris* Nees. According to H. L. Parker (1931*a*), the membrane of *Meteorus nigricollis* Thoms. remains in the egg shell after hatching, and on the seventeenth day after oviposition, which is about 10 days after hatching, it becomes dissociated into individual isolated cells, which float out into the blood of the host and increase considerably in size.

In *Opius tryoni*, *O. humilis* Silv., and *O. fullawayi* Silv., it has been observed by Pemberton and Willard (1918) that a gelatinous mass of cells clings to the ventral side of the body of the larva and usually persists until the first molt, when it is cast off with the exuviae. In *O. fletcheri*, the newly hatched larva is completely enveloped by this mass of cells, though it does not remain attached to the exuviae after the molt. The first-instar larva of *O. melleus* illustrated by Lathrop and Newton (1933) bears a large, rounded mass ventrally on the thorax, which may be of the same origin.

Ogloblin (1924) has made a detailed study of the membrane that surrounds the embryo of *P. coccinellae*. Through this membrane the embryo secures the food materials required for its development and the oxygen to fill its respiratory needs. At the time of hatching, the cells of the membrane are more or less cubical in form and measure 16 to 19 μ in diameter. Disintegration takes place at this time, and the cells float free in the blood of the host. They finally attain a diameter of 200 to 250 μ, which represents an increase in volume of 4,000 to 8,000 times the original size. In flowing with the blood stream, they tend to congregate in the posterior region of the abdomen of the host beetle, and the intermediate and mature larvae of the parasite, which feed upon these cells, usually lie with their heads at this point.

The most extended studies of this embryonic membrane are those of Jackson (1928, '35) on *P. rutilus* Nees in adult beetles of the genus *Sitona*. In some instances, it still encloses the larva after hatching; but dissociation takes place very soon thereafter, and the cells maintain an independent existence in the host body. They store up fats from the body fluids of the host and attain a maximum diameter of 0.1 mm. Eventually they are consumed by the parasite larva in its last stage. Paillot has found them in aphids which contained no parasite larvae but considers that, in these instances, the parasite larva itself had died and been completely absorbed.

Among the endoparasitic species, the habit of completing larval feeding after emergence from the host body has been frequently noted, particularly among the Cheloninae and Macrocentrinae. *Ascogaster quadridentata* emerges from the codling-moth larva and then entirely consumes the remaining body contents. In *Chelonus annulipes*, this external feeding phase is extensive and is essential to further development, for the cocoon cannot be spun unless such feeding has taken place. The larva of *C. blackburni* Cam. emerges from its host when only half-grown. All the species of *Macrocentrus* that have been studied have the external feeding phase, and emergence from the host body coincides with the third molt. The same habit has been observed in *Bassus hawaiicola* Ashm. In the Microgasterinae, only a very few species are known to feed after emergence from the host body. Among these are *Apanteles* sp. on *Nacoleia octasema* Meyr. in Java, *A. aristoteliae* Vier. in *Argyrotaenia citrana* Fern., and *Microgaster tibialis* Nees. The solitary *Apanteles* larvae completely consume the body contents of the host within a very short period after emergence.

Pupation.—The pupation habit of several species of *Rogas* differs from that of other members of the family which attack lepidopterous larvae, in that the cocoon is spun within the empty skin of the host. Just prior to the formation of the cocoon, the mature larva breaks the host skin

ventrally and pushes out that portion of the body contents which has not been consumed, and this material dries and fastens the host remains securely to the substratum. Some species, however, do not make this ventral break in the host skin.

The Vipioninae usually spin individual cocoons within the cell, cocoon, or leaf roll inhabited by the host, and in particularly confined quarters, as in a tunnel in wood or bark, they may be formed in line. *Microbracon* sp. on the larva of *Hapalia* in India does not form individual cocoons; instead, the group of larvae spin a thin common web and then pupate in a row beneath it.

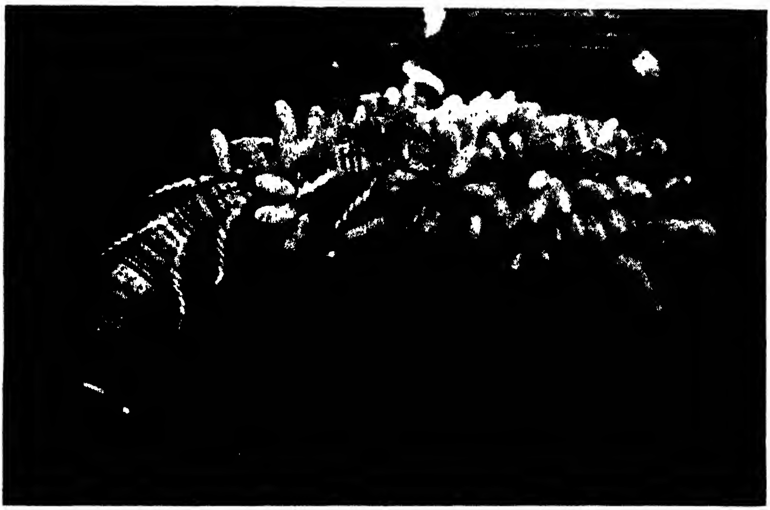


Fig. 12.—A larva of the tobacco hornworm parasitized by *Apanteles congregatus* Say. Some of the larvae are just emerging from the body, while others are in various stages of cocoon formation. (*Photograph by M. C. Swingle.*)

The Aphidiinae, with occasional exceptions, pupate within the empty skin of the aphid host, which is first lined with silk. Emergence is effected by cutting away a circular cap in the dorsum of the abdominal wall. A striking exception to the above occurs in *Praon simulans* Prov., the habits of which have been described in detail by E. W. Wheeler (1923). The mature larva leaves the body by an opening made in the venter of the abdomen and spins a tent-like covering beneath it, firmly attaching it to the leaf surface, and the compact spherical cocoon is then spun beneath the host remains and within this shelter (Fig. 12).

A considerable variation is shown in the position taken by the larvae of the Microgasterinae at the time of pupation. The solitary species of *Apanteles* may spin the cocoon beneath the body of the host or apart from it, whereas an undetermined species attacking the larva of *Nacoleia* in Java spins it within that of the host. Some gregarious species, such as

A. congregatus Say, spin the cocoons separately upon the body of the host at the point of emergence from the body, and standing perpendicularly, whereas those of *A. glomeratus* and *A. sagax* are found in irregular masses upon the leaf about the host body. According to Green (1925), the cocoon mass of *A. acherontiae* may be 3 in. in diameter, and the 1,200 or more pupae contained within it do not have definite individual cocoons. *Microgaster alvearias* F. has the unusual habit of forming its cocoons in orderly horizontal tiers, one above the other, like a pile of bricks; those of *A. militaris* and *Microplitis ceratomiae* Riley are in compact masses, standing vertically upon the substratum. The solitary cocoon of *M. maculipennis* Szep. is formed beneath the caudal portion of the host body.

Many species of *Meteorus* suspend the cocoon by a slender thread from the leaf or twig, and in *M. pulchricornis* this thread may be 8 in. in length. Immediately after its emergence from the host body, the larva spins a small mat of silk upon the substratum and then lets itself down by a thread from its mouth. Following this, the larva reverses its position, grasps the thread with the tip of the abdomen, and then completes the spinning of the cocoon. Owing to this manner of spinning, which is common to all species forming such cocoons, the head of the pupa is always downward, at the end of the cocoon opposite the point of attachment of the thread.

Cedria paradoxa has a rather unusual pupation habit; the group of larvae that develop upon a host build a common sheet-like cover of circular outline upon the leaf, and the individual cocoons are formed beneath this cover. There is usually a central row of cocoons encircled by others, which are arranged radially, with the heads directed outward.

In the Euphorinae, the most frequently encountered species, *Perilitus coccinellae*, forms its spindle-shaped cocoon longitudinally beneath the body of the living host beetle, with the legs of the latter entangled in the outer strands. Davis (1928) describes the reactions of parasitized *Hippodamia* beetles when freed from the cocoon. They rush about frantically, apparently in search of the cocoon, and when it is found they settle down upon it and attempt to entangle their legs once again in the web of loose silk surrounding it. Captivity is apparently voluntary, even at the time the cocoon is spun. *Microctonus melanopus* spins its cocoon beneath the host beetle in the same way, though several gregarious species of this genus form them en masse in the soil.

Ascogaster and *Chelonus* spin their cocoons within those of the hosts or in the cells occupied by the latter. Those of *Sigalphus bicolor* are closely packed in the host cocoon and are oriented so that their axes are nearly perpendicular to that of the host. The cocoons of *Macrocentrus abdominalis* are formed side by side, and all are oriented in the same

direction. The Opiinae and Alysiinae, which reach larval maturity in the host puparia, do not spin a cocoon.

Among the species of *Opius* and *Alysia* that have been studied, it appears that the meconium, which is normally cast by the mature larva or prepupa in the pupation cell or cocoon, is retained and is voided only by the adult. This is true also of *Alysia*, which likewise emerges from the puparium of its dipterous host. The last larval exuviae of *Opius* are consistently found upon the dorsum of the pupa rather than pushed to the posterior end of the puparium.

Mention is made by Jackson of the casting of the meconium by the mature larva of *P. rutilus* before pupation. It is enclosed in a long, membraneous sac which previously had lined the mid-intestine. This is apparently the "peritrophic sac" that has been studied in some detail by Clancy in *Helorus paradoxus* Prov.

The few solitary species of the family which pupate within the skin of the larval host usually orient themselves with the head toward the posterior end, whereas those which transform within dipterous puparia lie in the reverse position.

The Life Cycle.—The life cycles of the great majority of Braconidae are relatively short, particularly among the external parasites, for their development is not correlated with that of the host. Information is available regarding a considerable number of species of Vipioninae, largely of the genus *Microbracon*, and these have many generations each year. The incubation period covers 1 or 2 days, the larval feeding period 1.5 to 7 days, and the cocoon stage 4 to 8 days. The minimum cycle from egg to adult is 7 to 9 days, recorded for *M. lefroyi* Ashm. and *M. serinopae* Ramkr. in India. *M. sordidator* Ratz. has the exceptionally long cycle of approximately 56 days. Harries (1937) points out the marked differences in the cycle of *M. hebetor* under different temperature conditions, it being complete in 8 days at 32°C. and extending to 39 days at 16°.

The Euphorinae usually have several generations each year, though several species of *Microctonus* are said to have only one. In *Perilitus*, the egg stage covers 4 to 10 days, the larval period 14 to 20 days, and the cocoon stage 6 to 20 days, giving a total of 24 to 50 days from egg to adult. The Meteorinae have a somewhat longer cycle, *Meteorus cinctellus* Nees having only one generation per year, though *M. nigricollis* reaches maturity in 45 days after oviposition.

In the Microgasterinae, for which information is most nearly complete on a number of species of *Apanteles*, there are usually several generations each year, with the egg, larval, and cocoon stages covering approximately 2 to 5, 6 to 15, and 5 to 10 days, respectively. The minimum cycle is 10.5 days recorded for *A. marginiventris* Cress. The larval period of

Microgaster is somewhat longer than that of *Apanteles*. Among the Aphidiinae, *Lysiphlebus testaceipes* Cress. and *Aphidius gomezi* Quiles complete their cycles in 7 days, but others of the subfamily require 10 to 30 days.

Apanteles solitarius Ratz. has one generation, and a partial second, each year upon the satin moth, but the species is distinguished by having two distinct methods of passing the winter period (D. E. Parker, 1935). A portion of the brood hibernates in the mature larval stage in the cocoon, and the adults appear in early May. They attack host larvae coming out of hibernation at that time, and the second brood of adults appears about one month later. A portion of the overwintering population remain in the first larval stage within the living host caterpillars. Their development in the spring is rapid, and the adults appear only slightly later than those which develop from larvae that have hibernated in the mature form in the cocoons.

The life cycles of the Cheloninae, Macrocentrinae, Opiinae, and Alysiinae are, to a considerable extent, dependent upon the development of the host, inasmuch as larval feeding is completed only when a certain stage of the host is attained. Thus *Chelonus* may have a single generation each year upon one host, which itself has an annual cycle, whereas it may have several generations upon a multibrooded host. Fink and Daniel have both pointed out that development of *Macrocentrus ancylivorus* Roh. is delayed in small host individuals and that this effect extends even to a prolongation of the incubation period. The Opiinae and Alysiinae complete their larval development only after their dipterous hosts have attained the pupal stage. Some of the parasite individuals may consequently attain the pupal stage at a time when others of the same age are still first-instar larvae. *Alysia manducator* has a considerably longer life cycle than its host, resulting in the production of only two generations each year as compared with four for the host.

The majority of endoparasitic species of the family pass the winter as first-instar larvae within the living hosts. This applies to most species of *Apanteles*, though a few of these, such as *A. glomeratus* and *A. solitarius*, may at times be in the mature larval stage in the cocoon, and to the Euphorinae, *Triaspinae*, and some Meteorinae and Braconinae. The polyembryonic *Macrocentrus gifuensis* hibernates in the morula stage within the living host, whereas *Aphidius fabarum* Marsh hibernates in the pupal stage within the cocoon, as does *Cardiochiles nigriceps*. *Cedria paradoxa* is the only representative of the family known to hibernate as an adult female. These females mate in the autumn, and the males do not survive the winter.

The Opiinae, which pass the winter in the mature larval stage in the host puparia, exhibit a pronounced tendency in that stage to go into

diapause. In *Opius tryoni* and *O. fullawayi* slightly more than 1 per cent of the larvae may persist for several months at a mean temperature of about 24°C., and in exceptional cases the diapause may extend to nearly one year. This tendency is even more pronounced in *O. melleus*, in which a portion of the brood normally carries over to the second year or later (Lathrop and Newton, 1933). From a quantity of parasitized host puparia collected in 1925, 78.6 per cent of the parasites emerged the following year, 20.3 per cent the second year, and 1.1 per cent the third year.

An obligatory alternation of hosts occurs in several species of *Apanteles* and in occasional species of other groups. The stages of each host that are subject to attack are present in the field for only a small portion of the active season, and consequently they can support only one parasite generation. The second must of necessity be upon one or more alternate hosts having a different seasonal cycle. Parasite species that are incapable of passing the winter in the adult or cocoon stage must have one or more hosts that persist as larvae during this period. Thus *A. lacteicolor*, which was imported into the United States as a parasite of the brown-tail moth, passes the winter in young caterpillars of that host, but its summer generations are in young gypsy-moth caterpillars and in those of several native species (Muesebeck, 1918). In Japan, *A. liparidis* Bouché goes through two generations in gypsy-moth larvae during the summer, and the overwintering generation then carries over in *Dendrolimus* larvae (Burgess and Crossman, 1929). According to Muesebeck, *Meteorus versicolor* has a seasonal cycle and alternation of hosts similar to that given for *A. lacteicolor*.

In *Microtonus brevicollis*, the alternation of hosts is much more striking than that described above, for the alternate broods are in different stages of the same host rather than in the same stage of different hosts. According to Kunckel D'Herculais and Langlois (1891), the overwintering generation is contained in adult beetles of *Haltica ampelophaga* Guer., whereas the summer generation develops exclusively in the larvae of that species. This is comparable to the cycle of the tachinid, *Erynnia nitida* R.D., a parasite of the elm leaf beetle, *Galerucella luteola* Mull., in Europe.

Reproductive Capacity.—The reproductive capacity is comparatively high in many species of the family, particularly those which develop internally in the host. The ovaries of a gravid female of *Apanteles glomeratus* are said to contain upward of 2,000 eggs, and 15 to 35 are deposited at one insertion of the ovipositor. A single female of *A. melanoscelus* deposited 535 eggs in a period of six days, and it was estimated by Crossman that the capacity of this species under field conditions is approximately 1,000. *Microgaster marginatus* has 900 to 1,000

mature eggs in the ovaries within two weeks after emergence. Among the Aphidiinae, the egg production is also high. Females of *Lysiphlebus testaceipes* may contain as many as 430 eggs at one time, and it is reported by Perez (1930) that *Aphidius gomezi* has a capacity of 1,500. Nearly 600 aphids were parasitized in one day, and approximately 1,000 progeny were secured from a single female. The egg-ovipositing species of the family usually have a high reproduction capacity, as shown by the deposition of 655 eggs by a female of *Chelonus annulipes* in 22 days, with 156 remaining in the ovaries at death. Another female deposited 165 eggs in a single day (Vance, 1932*b*).

The polyembryonic species of Macrocentrinae, which produce upward of 50 individuals in each host, deposit 200 to 300 eggs, and they consequently have a reproductive potential of several thousand.

The ectoparasitic Braconidae, of which a number of species of the genus *Microbracon* have been carefully studied, range from a minimum of 80 eggs for *M. greeni* Ashm. to the 678 recorded by Taylor (1932) for *M. brevicornis* upon *Heliothis armigera* Hbn. in South Africa. An unusually low reproductive capacity is indicated for *Ischiogonus syagrii*, in which the ovaries were never found to contain more than 12 mature eggs at one time.

The number of parasite individuals that are able to develop to maturity in a single host is often high. Green (1925) reports that a total of 1,226 adults of *Apanteles acherontiae* Cam. emerged from a single cocoon mass and that several hundred still remained. All these had developed in a larva of the hawk moth, *Acherontia lachensis* F. A maximum of 129 *Apanteles liparidis* is recorded from a larva of *Dendrolimus* (Burgess and Crossman, 1929). The euphorine parasites of adult beetles are usually solitary; yet McColloch records the development to maturity of 124 larvae of *Microctonus eleodis* Vier. in one *Eleodes tricostata* Say.

The influence of temperature upon the reproductive capacity has been studied by Payne (1933 to 1934) in the case of *M. hebetor*, and the reproductive potential was found to be 67.5 at 36°C. and 90 at 27°C., and it then declined to 28 at 15°C.

The effect of temperature and food conditions upon the parasite adults is reflected in several ways. Donohoe has found that the development of *Microbracon hebetor* at temperatures fluctuating between 10 and 26.7°C. results in adults which are glossy black in color, whereas at 26.70° they are mostly dark-brown to black and at 32° the color is pale brownish-yellow to brownish-orange. In *Sycosoter lavagnei*, according to Lichtenstein and Picard (1917) and Picard (1919), there is a seasonal dimorphism in both sexes, in which only the apterous forms are found early in the spring, winged females and a preponderance of winged males

in midsummer, and the apterous forms of both sexes in great majority during the autumn. Temperature is considered to be the most important factor influencing this cycle, though the quantity and quality of food at different seasons contribute to the change.

Polyembryonic Reproduction.—The occurrence of this mode of reproduction in the Braconidae was first suspected by Voukassovitch (1927*b*) in the case of *Macrocentrus abdominalis*, parasitic in caterpillars of *Psammotis* and *Tortrix* in Europe. In each of these hosts, 17 to 41 parasites reach maturity, and it was noted, among 25 broods, that 13 comprised females only, 8 were males only, and 4 broods were mixed. Actual proof of polyembryonic reproduction was presented by H. L. Parker (1931*b*) in the case of *M. gifuensis*, a parasite of the European corn borer, which for a time was confused with *M. abdominalis*. The broods range in size from an average of 16 in pure broods of females to 24 if all are males. Among 200 broods for which records were taken, 71 consisted exclusively of males, 54 of females, and 75 were mixed. The mixed broods are considered to be the result of duplicate oviposition.

The egg of *M. gifuensis* transforms to a spherical pregerm, which is usually lodged in a fat cell, and this grows to a primary germ, which divides by fission. The secondary germ continues division, forming tertiary germs, eventually resulting in morulae which finally develop into embryos and into first-instar larvae. There is no blastula stage, and no proliferation of host tissue to form a cyst about the parasite body such as occurs in the development of certain chalcidoid and serphoid Hymenoptera of polyembryonic habit.

Daniel (1932) has made an extended study of *M. ancylivorus*, a solitary internal parasite of a number of species of lepidopterous larvae, and has found that development to the embryo stage is similar to that described by Parker for *M. gifuensis*. In this case, however, the first parasite body to attain the larval stage exerts an inhibitory influence upon the remaining embryos, morulae, germs, and pregerms that are present in the host body, and no further development of these takes place. The action is not mechanical but is considered to be due to the secretion of some substance by the larva or by the host through the influence of the parasite larva. Where two or more larvae develop simultaneously, the death of all but one is brought about by combat. In this species, polyembryonic reproduction does not achieve its purpose, for only a single individual attains maturity from any one egg deposited. It is probable that *M. ancylivorus* was at one time parasitic upon a much larger host in which a number of progeny could develop in each; but in its present hosts, so far as they are known, it is consistently solitary.

Amicroplus collaris Spin., which attacks the larvae of *Euxoa segetum* Schiff. in Europe, has recently been recorded by Paillot (1937) as repro-

ducing polyembryonically. Two or three eggs are deposited at each insertion of the ovipositor, and 40 to 50 individuals develop to maturity in each host.

Information available regarding the number and sex of the broods of other species of Braconidae points to the possibility of polyembryonic reproduction in *M. crambivorus* Vier., in which the broods are reported to be of one sex only, and in *Sigalphus bicolor* Cress. studied by Cushman (1913*a*), of which as many as 30 may reach maturity in a single caterpillar of *Apatela* and nearly half of the broods are of one sex only.

Sex Ratio and Parthenogenesis.—The known sex ratios in the Braconidae show an exceptional number of species that yield a preponderance of male progeny and only a small number that have a large majority of female progeny. Various figures have been given by authors for the ratio in *Microbracon hebetor*, ranging from 3:1 to 1:2. Payne (1934) found that the proportion of males is higher under low temperatures, and she ascribes this to a decrease in mating activities. In *M. terebella* Wesm., the normal ratio is approximately 2 to 1, with 62.6 per cent of the colonies comprising females only, 26 per cent males only, and 11.4 per cent of both sexes (Salt, 1931*b*). The colonies comprise an average of 3.3 individuals, those of the males numbering 3.9 and of the females 2.9. *Cedria paradoxa* was found to have a sex ratio of 5.5 to 1 in both China and India and upon different hosts. A preponderance of females is shown also in *Lysiphlebus testaceipes* and *Sigalphus bicolor*, the figures being approximately 2 to 1 and 3.4 to 1, respectively. *Heterospilus cephi* Roh. and *Macrocentrus gifuensis* show the males slightly in the majority, whereas in *M. ancylivorus* the females predominate in the ratio of 3 to 2. *Opius fletcheri* has the females slightly in the majority, whereas other species of that genus have that sex in the minority, the extreme being 1 to 2 in *O. melleus*.

Holdaway and Smith report a marked variation in the sex ratio of *Alysia manducator*, which is correlated with the size of the hosts. The small puparia of *Lucilia sericata* Meig. yield only males, whereas the largest hosts, of *Calliphora vomitaria* L., give females almost exclusively. Within each host species, as well as between species, the sex ratio varies consistently, the larger puparia yielding a greater proportion of female parasites than do those of smaller size.

An unusual condition has been pointed out by both Fink (1926) and Stearns (1928) in regard to the male progeny of unmated females of *M. ancylivorus*. These are stated to be only half as large by weight as the males produced by mated females.

Unisexual reproduction is normal in a number of species of Braconidae, among which may be mentioned *Apanteles thompsoni*, *Meteorus japonicus* Ashm., *P. coccinellae*, *Microctonus brevicollis*, and *Rogas unicolor* Wesm.

Not a single male of *A. thompsoni* has ever been secured in the large-scale rearings that have been made. Many workers in Europe and North America have collected and reared *P. coccinellae;* yet it was only recently that the first authentic male was recorded. Extended rearings of field material of *R. unicolor* showed that the males consistently represent less than 1 per cent of the population (Dowden, 1938). Mating takes place readily, though this is not essential, as virgin females reproduce the same sex. Only a single male was reared experimentally, and this individual was the progeny of an unmated female.

Although the capacity to reproduce parthenogenetically appears to occur generally throughout the family, yet in occasional species mating appears to be essential to the production of progeny. MacGill (1923) found that eggs produced by virgin females of *Aphidius avenae* Hal. consistently failed to hatch.

M. brevicollis is said to produce a summer generation that is exclusively females in larvae of *Haltica,* and the overwintering generation in adult beetles gives rise to adult parasites of both sexes. In the case of *Lysiphlebus testaceipes,* Hunter (1909) and Webster and Phillips (1912) have demonstrated that, though males are normally produced by virgin females, yet occasional females appear. Hunter states that these represent 1.7 per cent of the progeny, whereas the latter authors record that 4 in 48 unmated females produced some female progeny. In each case, these represented only a very small portion of the brood, and exclusively male progeny resulted in the second generation. Whiting (1921) has shown that unmated females of *Microbracon hebetor* likewise produce occasional females.

EFFECT OF PARASITISM UPON THE HOST

The development of the parasite larva within the host body brings about a number of changes in the latter which are revealed externally before death. In the case of *Ascogaster quadridentata,* the parasitized larvae of the codling moth found in the cocoons and that have completed their feeding are only one-fourth to one-third of normal size and are whitish rather than pink in color. The hosts of many Microgasterinae show a similar difference in size as compared with healthy larvae. In contrast to this, Beeson and Chatterjee mention that the larvae of Sphingidae parasitized by *Megarhogas theretrae* Vier. become nearly double their normal size before death. Upward of 50 parasite larvae develop in each host. This inflation of the host body brings to mind the similar condition that occurs in caterpillars parasitized by species that reproduce polyembryonically. European-corn-borer larvae containing advanced larvae of *Meteorus nigricollis* are a dirty brown in color, and an examination of the internal organs reveals that the fat body bears

numerous wounds, apparently inflicted by the parasite larva. Haeussler (1932) mentions that larvae of *Grapholitha molesta* Busck parasitized by *Macrocentrus ancylivorus* are retarded in their development and that the parasite emerges from the body an average of three days later than the time at which healthy larvae pupate. The dipterous hosts of the Opiinae complete larval development and usually form a normal puparium, though the pupal stage is never attained.

It has already been pointed out, regarding euphorine and other parasites of adult beetles, that death of the host may not take place until some time after the emergence of the parasite larva from the body. This is true also in the case of many lepidopterous larvae attacked by internal parasites of the subfamily Microgasterinae. According to Gatenby (1919), the larvae of *Pieris brassicae* accomplish a partial recovery after the emergence of the brood of *Apanteles glomeratus*, and some have been known to survive for one month. "Examination of haemocoelic fluid of parasitized larvae failed to reveal any very obvious differences when compared with the blood fluid of non-parasitized caterpillars." In case only a few parasite larvae develop in the body, the host may attain the pupal stage after their emergence, and possibly even the adult stage. Grandori (1911) and Faure (1926) also mention the attainment of the pupal stage by some individuals. In contrast to this is the death of the brown-tail-caterpillar host prior to emergence of the larva of *A. lacteicolor* from its body (Muesebeck, 1918). This is due to the destruction of a portion of the central nervous system. A solitary parasite such as this, developing in a very young host, naturally consumes a greater portion of the body contents and consequently causes greater injury than do a number of individuals in a nearly mature caterpillar.

The effect of parasitism upon the host is of particular interest in those cases in which the adult stage of the host is attacked, or is attained before death. The parasite groups involved are largely the subfamilies Euphorinae and Aphidiinae, the former being known principally for its attack upon adult beetles and the latter upon aphids. Observations on the effect of *Perilitus coccinellae* parasitism upon coccinellid adults have been made by Balduf (1926*b*). The host usually does not die for some time after the emergence of the larva from its body. Parasitized females very seldom show the ovaries to be in a functional condition, and in females that are gravid at the time of attack they are disrupted. No fatal injury is inflicted by the parasite larva, either through its feeding or by mechanical injury at the time of emergence, but the host is considerably weakened and dies from starvation because of entanglement in the outer strands of the parasite cocoon, which is formed beneath its body. Timberlake (1916) found that the more vigorous beetles of *Olla abdominalis*

Say recovered completely if freed from entanglement with the cocoon and resumed feeding and oviposition. In some instances, these beetles were again parasitized experimentally and yielded mature larvae. Full recovery from the effects of parasitism requires considerable time, and one female began depositing eggs after a lapse of 22 days from the time the parasite larva emerged from her body.

Adult beetles of *Sitona* spp. parasitized by *Perilitus rutilus* show the female reproductive system to be atrophied, whereas the male organs are still functional at the time of emergence of the parasite larva.

Kurdjumov and Znamenski (1917), McColloch (1918), and Speyer (1925) have noted the effect of *Microctonus* upon its hosts. The first-named authors state that sterility is produced in the overwintering flea beetles, but those which are attacked in the early spring deposit the greater portion of their eggs before their reproductive activities are affected by the parasite. McColloch mentions that one female of *Eleodes tricostata* Say deposited three eggs on the same day that 124 mature larvae of *M. eleodis* emerged from her body. Speyer's observations upon what was probably a species of *Microctonus*, in *Ceutorrhynchus*, indicate that host oviposition takes place normally until an advanced stage of development is attained by the parasite larva and that the principal effect upon the internal organs is in the degeneration of the fat body. In *Cosmophorus henscheli*, it was found by Seitner and Notzl (1925) that mating by the adult beetles of *Pityophthorus* was not inhibited, though the female organs were atrophied. No eggs or larvae were found in the brood chambers of parasitized beetles.

The effect of parasitism upon aphids by the Aphidiinae is greater than that upon beetles by the Euphorinae, owing principally to the fact that oviposition by the parasite frequently takes place before the adult stage is reached. According to Hunter (1909), nymphs of *Toxoptera graminum* Rond., if parasitized by *Lysiphlebus testaceipes* Cress. (*tritici* Ashm.) during the second stage, attain maturity before death but do not reproduce. When they are stung after the fourth molt, two to six young may be produced. Webster and Phillips (1912), in observations upon the same parasite, found that stinging in the first two nymphal stages resulted later in death of both the host and the parasite larva, and they quote results similar to those given above for *T. graminum* in case of attack at a later stage. In the case of *Aphidius rapae* Curt., it was found by Spencer (1926) that, irrespective of the stage of development of the embryos in the body of the host aphid (*Myzus* and *Aphis*), their growth is arrested at the time the parasite egg hatches and they finally disintegrate. The development of winter eggs is likewise inhibited. The production of eggs or nymphs ceases on the third day after oviposition by the parasite, this period representing the time required for incubation

of the egg. Extensive physical changes take place in the host body before death. The parasite embryo is said to secrete a cytolytic enzyme which aids in breaking up the serosa; it is also believed to be responsible for the death of younger larvae of its own species, for the abstraction of food materials from the fat body, and for the stoppage of development of the host eggs or embryos. In the final larval stage of the parasite, the embryos and eggs are first consumed, and then the remaining body contents.

In *Lucilia* and other dipterous hosts of *Alysia manducator*, it has been found that parasitism has a pronounced influence upon the physiological processes involved in pupation. This is not a result of the activities of the parasite larva in the body but is a direct consequence of stinging at the time of oviposition. The hosts normally pass the winter as mature larvae; yet those which are parasitized always pupate in the autumn. Some toxic substance injected at the time of stinging apparently provides the stimulus for premature pupation. The occurrence of unparasitized puparia among host material collected during the winter is explained by their having been stung but not successfully parasitized.

In a study of the effect of parasitism of caterpillars of *Cirphis unipuncta* How. by *Apanteles militaris*, Tower (1916) determined that individuals parasitized shortly after the fourth molt ate less than half as much foliage during the period between attack and emergence of the parasite larvae from the body as did unparasitized individuals.

An incidental effect of parasitization of *Ephestia* by *Microbracon hebetor* is infection by a disease organism *Thelohania ephestiae* Mattes, wherein the female parasite serves as the vector (Payne, 1932). The first foci of the disease occur in the thoracic ganglia that have been pierced by the sting of the parasite. Later the sporozoan is found throughout the nervous system and the fat body. The disease cannot be transmitted by mouth, and no infection results from contact of healthy larvae with those which are diseased.

IMMATURE STAGES

The Egg.—The general form of the eggs of the Braconidae is simple, ranging in outline from broadly oval to almost cylindrical but frequently somewhat pear-shaped, or elongate and tapering at both ends and usually without a stalk or pedicel. The egg of *Microbracon lendicivorus* (Fig. 13*B*) differs from those of other Vipioninae in having a slender tapering stalk, slightly longer than the egg body, at what is presumably the anterior end. In *Dendrosoter protuberans* Nees (Fig. 13*G*), the stalk is very broad and is bent back upon the egg body in a characteristic way, whereas, the stalk of *Coeloides subconcolor* Russo (Fig. 13*F*) is long and has a distinctly segmented appearance (Russo, 1938). Most of the species of *Apanteles* have a short peduncle at the posterior end, and *Opius crawfordi* K. & P. has this peduncle equal to or longer than the egg body. Other species of the latter genus lack the peduncle entirely

or have it in a very reduced form (Fig. 13*D*, *E*). The egg of *O. tryoni* is enveloped by a thin, transparent membrane, possibly the exochorion, which is broken during the period of incubation owing to increase in size of the egg. This recalls a similar egg envelope found by Dowden in *Brachymeria compsilurae* Cwf.

The Euphorinae have the stalk at the posterior end, and in some species of *Perilitus* it is nearly as long as the main body. The same is true in a number of species of Meteorinae. The egg of *Alysia manducator* (Fig. 13*C*) bears a pronounced button-like tubercle at its larger, presumably anterior end. Although the evidence is not complete and there are several apparent exceptions, it appears that the stalk of the braconid egg, when present, is usually situated at the posterior end. In no instance does it serve any definite purpose after deposition.

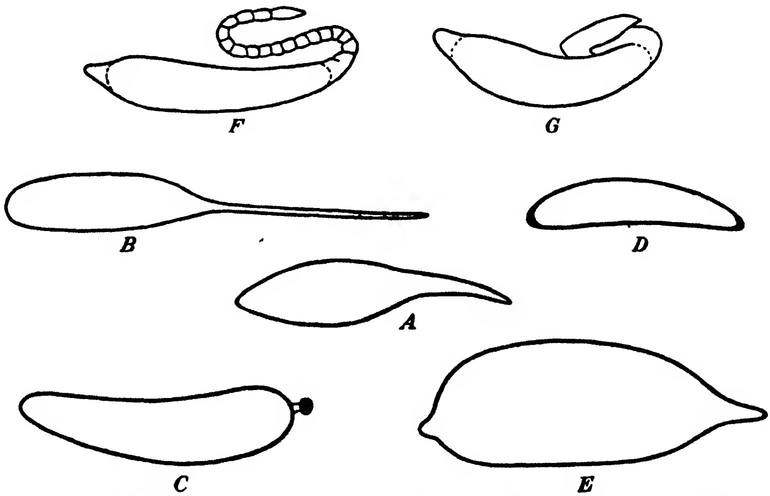


FIG. 13.—Eggs of the Braconidae. *A*, *Apanteles lacteicolor* Vier.; *B*, *Microbracon lendicivorus* Cushm.; *C*, *Alysia manducator* Panz.; *D* and *E*, freshly deposited and fully incubated eggs of *Opius humilis* Silv.; *F*, *Coeloides subconcolor* Russo; *G*, *Dendrosoter protuberans* Nees.

The eggs of *Ascogaster*, *Phanerotoma*, and *Chelonus*, which are deposited in those of the host, are of minute size, measuring 0.2 mm. or less in length. In all species of the family the chorion is thin and transparent, and usually has no surface sculpturing, though in *Meteorus versicolor* and *Microdus dimidiatus* it bears minute hexagonal markings.

First-instar Larvae.—The first-instar larvae of the Braconidae represent a considerable variety of forms, comprising the hymenopteriform, mandibulate, caudate, vesiculate, and polypodeiform. It is often debatable, particularly in reference to this family, as to whether a particular larva should be classed as mandibulate, caudate, vesiculate, or polypodeiform, for it may possess two, or in some cases three, of the characters upon which the grouping is based. The hymenopteriform larva has a medium-sized head, 13 body segments, which usually bear transverse bands or rows of setae, and spiracles on the first thoracic and the first eight abdominal segments. This type of larva is representative of the ectophagous forms, comprising the Vipioninae and representatives of the Braconinae and Hormiinae, and will doubtless be found in other groups. *Bracon* sp., probably *B. hylobii* Ratz., is distinguished by the lack of spiracles (Munro, 1917).

The mandibulate larvae are found generally in the Opiinae and, in combination with the caudate character, in the Euphorinae, *Triaspinae*, Alysiinae, and Pambolinae. Vesicle-bearing larvae of this type occur in the Macrocentrinae. The larva of *Opius tryoni* (Pemberton and Willard, 1918) is typical of the Opiinae and has a large, heavily sclerotized head, large falcate mandibles, and short, blunt antennae. A pair of fleshy finger-like processes is found ventrally at the anterior margin

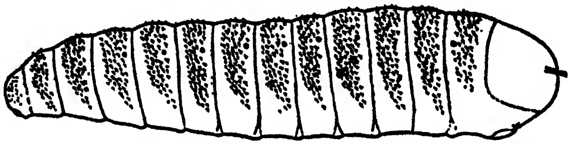


FIG. 14.—Hymenopteriform first-instar larva of *Heterospilus cephi* Roh. (*From Hill and Smith*, 1931.)

of the first thoracic segment. A well-defined tracheal system, with anterior and posterior commissures, is present and filled with air, but there are no spiracles. The larvae of *O. humilis*, *O. fletcheri* (Fig. 15), and *O. fullawayi* are very similar to that of *O. tryoni*. Keilin and Picado (1913) have made an extended study of the first-instar larva of *O. crawfordi* (Fig. 16*A*), which has an almost spherical head, a pair of very large mamma-like processes, each surmounted by three sensory papillae, on the first thoracic segment and a smaller conical-shaped pair on the third segment. These processes are on the concave side of the body, as is also the anal opening. The authors assert that the concave side of the body, to which the mouth opening is directed, is in reality the dorsum and support their conclusion by demonstrating the presence of the nerve cord along the convex side and of the heart on the concave side. Recognition of the markedly concave side of the first-instar larva as dorsal rather than ventral is also reported by Baume-Pluvinel (1914) in *Adelura gahani* B.-P. (Fig. 16*B*), which develops in the larvae of various Phytomyzinae. Further investigation of this interesting point in other species would be desirable.

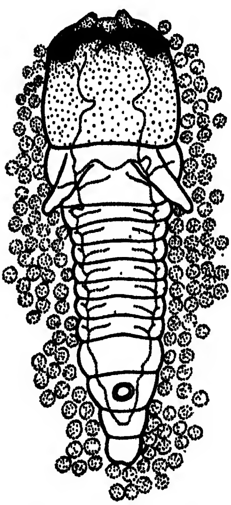
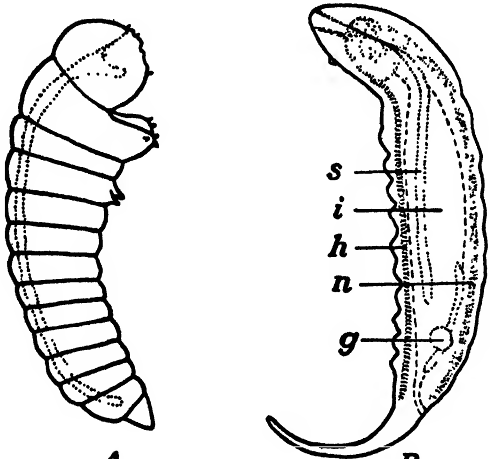


FIG. 15.—The first-instar larva of *Opius fletcheri* Silv., ventral view. (*From Pemberton and Willard*, 1918.)

The larva of *Ascogaster quadridentata* has an exceedingly large head and 13 body segments of diminishing width, with no tail or other fleshy processes, whereas *Chelonus annulipes*, which is of modified mandibulate form, has a short tail following the 8 or less distinct body segments. The larva of *Macrocentrus ancylivorus* is elongate in form and has a pair of short fleshy processes and a short caudal horn on the last segment. The anal vesicle is relatively small. In the Euphorinae the large, heavily sclerotized head, bearing the falcate mandibles at the front, is followed by 12 or 13 body segments of decreasing width and a rather short tail, which bears setae on the distal half or two-thirds.

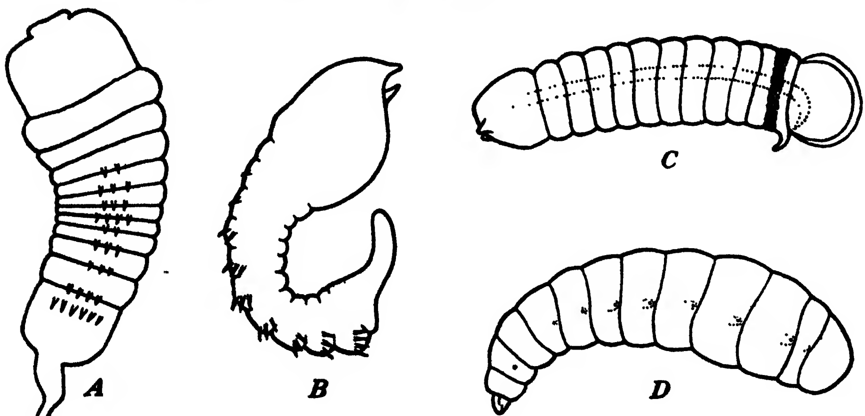
The true vesticulate larvae are found mainly in the subfamily Microgasterinae, of which the principal studies have been made in the genera *Apanteles* and *Microgaster*. At the time of hatching, many of these have the general appearance of mandibulate larvae, and they may bear a fleshy tail approaching half the length of the body proper. Usually only 10 or 11 ring-like body segments are distinguishable, the last segment apparently representing several that have fused. Each of the

segments usually bears a transverse row of setae dorsally. In *A. tasmanica* Cam. (Dumbleton, 1935) and *Microgaster tibialis* (Fig. 17*A*) (Vance, 1932*a*), the rows of setae are lacking on the first two segments, whereas in other species they are missing



A *B*

FIG. 16.—*A*, the first-instar larva of *Opius crawfordi* K. & P. showing the nerve cord on the convex side and the paired thoracic processes on the dorsum (*after Keilin and Picado*, 1918); *B*, first-instar larva of *Adelura gahani* B.-P. showing (*s*) salivary gland, (*i*) intestine, (*h*) heart, (*n*) nerve cord, and (*g*) genital glands. In this larva also the convex side, rather than the concave, is ventral (*after Baume-Pluvenel*, 1914).



A *B* *C* *D*

FIG. 17.—Immature stages of the Braconidae. *A*, first-instar larva of *Microgaster tibialis* Nees, dorsal view (*from Vance*, 1932); *B*, newly hatched first-instar larva of *Apanteles melanoscelus* Ratz., lateral view; *C*, second-instar larva of same, showing anal vesicle, caudal horn, and the first exuviae encircling the anterior portion of the eighth abdominal segment; *D*, third-instar larva of same (*from Crossman*, 1922).

on only the first segment. The vesicle appears shortly after feeding begins, and its width is then equal to or greater than that of the preceding segments (Fig. 17*C*). The body at this time is somewhat cylindrical, and the tail, which previously was prominent, now appears as only a small ventrally directed "horn" beneath the

vesicle. In *A. militaris* (Tower, 1915), *A. hyphantriae* Riley, and *A. thompsoni*, there is no indication of a tail structure at any time, and the bulb-like vesicle is well-developed even before hatching.

The wall of the proctodeum of the first-instar larva of *Orgilus obscurator* Nees is relatively thin (Fig. 18), but it increases greatly in thickness in the second instar (Thorpe, 1932).

The simple caudate type of larva, without other adaptive modifications, is found principally in the Meteorinae and Aphidiinae, whereas the tail in some form is present in practically all groups which develop internally. In *Meteorus*, there are 12 or 13 segments exclusive of the tail, and the latter may exceed the body in length, though in some species it is only one-eighth as long. Each segment usually bears a transverse row of setae on the dorsum, and the tail may also bear setae. The first-instar larvae of many of the Aphidiinae are recognizable principally by the possession of a row or comb of heavy setae at the posterior margins of each body segment and by the two ventrally directed lobes of the last segment. The tail in this subfamily is usually somewhat tubular in form with the distal end rounded. There are 13 distinct body segments. The fringe of spines at the posterior margin of each segment dorsally and extending to the lateroventral margins is, so far as known, found only in *Praon*, while in *P. simulans*, studied by Timberlake (1910), they occur only on the third thoracic segment and on all abdominal segments except the last. Janiszewska (1933) describes the larva of an undetermined Aphidiine, believed to be *Aphidius*, in which this row or comb of spines is present on each body segment. In *Ephedrus incompletus* Prov. (Wheeler, 1923) and other species of the genus, the larva (Fig. 19) bears on each segment a median transverse ridge which is more pronounced on the dorsum and sides and is strongly serrate, with the teeth directed caudad. The tail also is heavily and completely spined, with the spines arranged in rings about it. These adaptations are possibly locomotory in function. The ventrally directed bilobed process of the caudal segment is found in *Praon*, in *Ephedrus*, and in some species of *Aphidius* and consists of two conical or finger-like processes, about the length of one segment, situated ventrally at the base of the tail. The majority of the species of the genus *Aphidius* have simple caudate larvae, which lack entirely the integumentary spines and the paired caudal process, and the tail is only lightly spined on its distal portion. Larvae of the Aphidiinae have the anal opening ventrally at the base of the tail rather than dorsally; in the species having the lobed processes, it is situated between the bases of the lobes and the tail.

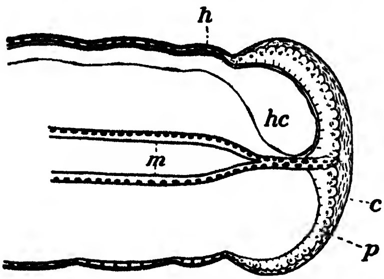


FIG. 18.—The anal vesicle of *Orgilus obscurator* Nees, showing (*c*) the chitinous cuticle, (*h*) hypodermis, (*hc*) heart cavity, and (*p*) proctodeum. (*Redrawn, after Thorpe*, 1932.)

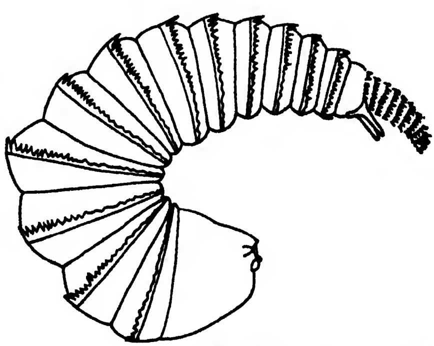


FIG. 19.—The first-instar larva of *Ephedrus incompletus* Prov. (*From Wheeler*, 1923.)

The polypodeiform larva is found in isolated species in a number of subfamilies. That of *Dacnusa navicularis* var. *cynaraphila* Ric. (Ricchello, 1928) (Fig. 20*A*) is, except for its paired ventral processes, typically caudate, with a transverse row of setae dorsally on each abdominal segment. The paired ventral processes occur upon each of the 12 body segments and are surmounted by a group or row of setae. The larva of *D. areolaris* (Fig. 20*D*), on the other hand, lacks the tail and the paired ventral processes (Haviland, 1922*a*). *Bassus dimidiator* (Fig. 21) (Silvestri, 1923*a*), *B. pumilis* Ratz. (Thorpe, 1933), *B. stigmaterus* Cress., and *Macrocentrus gifuensis* are distinguished by having two pairs of fleshy processes on each segment. In *M. gifuensis*, these are present on the first 12 segments and are of uniform size, whereas in the first two species named they are lacking on the first segment and are of slightly greater size on the abdomen.

The respiratory system of first-instar larvae of certain of the endoparasitic species, such as the Opiinae, consists of the two lateral trunks with branches at the various

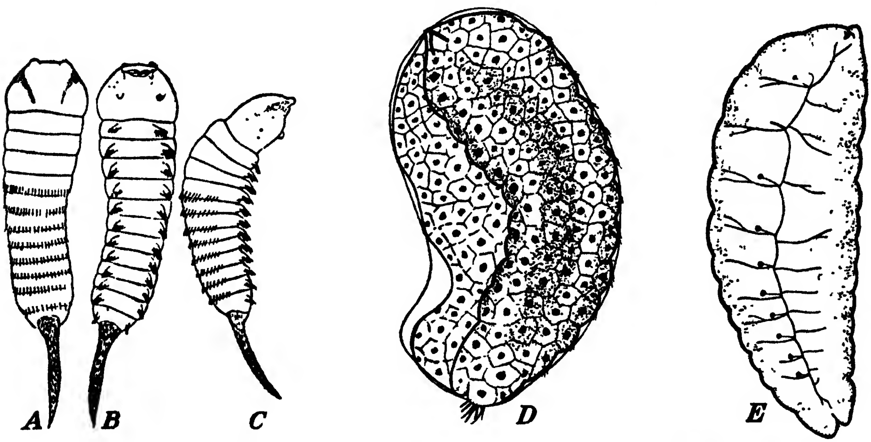


FIG. 20.—Immature stages of Braconidae. *A*, *B*, and *C*, the first instar larva of *Dacnusa navicularis* var. *cynaraphila* Ric., showing the paired ventral processes on the body segments (*from Ricchello*, 1928); *D*, first-instar larva of *D. areolaris* Nees before rupture of the trophic membrane; *E*, third-instar larva of same (*from Haviland*, 1922).

segments and an anterior dorsal and a posterior ventral commissure. In a considerable number of species, however, there is a complete lack of the tracheal system in this instar.

In the great majority of species, the mandibles are simple, though several exceptions occur. Those of *Microbracon brevicornis* are 5-dentate on the lower border, whereas in *Bracon tachardiae* they are 4-dentate, the teeth being long and spine-like, and in *Heterospilus cephi* (Hill and Smith, 1931) the main tooth is followed by five or six elongate teeth in comb-like arrangement along the inner edge. It will be noted that these departures from the normal are in species which feed externally.

Intermediate- and Final-instar Larvae.—The intermediate larval instars of the ectoparasitic species do not differ in any essential character from the first instar. Among the internal parasites, the mandibulate-type larva loses the large, heavily sclerotized head, with its long falcate mandibles, at the first molt, and in the caudate forms the tail is reduced in size with each succeeding molt and is entirely lacking in the last instar. In some species having five instars, it disappears after the second molt, and in *Cosmophorus henscheli* it is entirely absent in the second and following instars.

Many first-instar *Apanteles* larvae have a tail, or "caudal horn," situated beneath the vesicle, which in some species disappears entirely at the first molt and in others persists in reduced size in the second-instar larva. In contrast to this, the anal vesicle of the larvae that possess it increases in size with each molt but is absent in the final instar. In *A. thompsoni*, it is said to persist for only a short time after the second molt. The paired ventral processes on the last segment of many aphidiine larvae do not persist beyond the first instar. Many species reveal an increasing number of small teeth on the inner margin of the mandibles in the intermediate instars. In *Bracon tachardiae* Cam., the four teeth of the first instar are succeeded by five in the second and third, whereas the mandibles of *Microbracon mellitor* Say are simple in all instars.

The paired ventral processes that occur on the bodies of first-instar polypodeiform larvae, such as those of some species of *Bassus* and of *Macrocentrus gifuensis*, persist in much reduced form in the second instar. According to Parker, the larva of the latter species lacks mandibles in this instar.

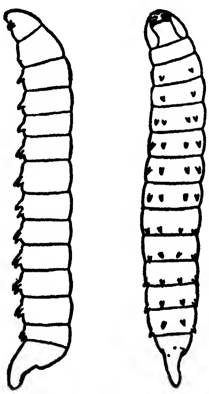


Fig. 21.—The first-instar larva of *Bassus dimidiator* Nees, lateral and ventral views. (*From Silvestri*, 1923.)

The mature larvae of the Braconidae are of normal form and have few characters that distinguish them, aside from the tracheal system. In many species, the mandibles have minute teeth, often slender and spine-like, on the inner margin, approaching 30 in number in some species, giving a comb-like appearance. Voukassovitch, in describing the mature larva of *M. abdominalis*, mentions a bilobed chitinous "anal capsule," of which the ventral lobe is more heavily sclerotized and bears a small ventrally directed process. The anal opening is between the two lobes of the capsule. Beeson and Chatterjee refer to a prominent "process" ventrally on the fifth and sixth abdominal segments of the larva of *Perilitus mylloceri* Wlkn. but do not otherwise describe it.

The mature larvae of many of the ectophagous species bear a dense coating of fine hairs; in some instances, this is uniform over the body, and in others it occurs in a transverse band on each segment and may be absent ventrally.

It has already been pointed out that the respiratory system of the ectoparasitic first-instar braconid larva has normally nine pairs of spiracles, situated on the first thoracic and the first eight abdominal segments. In these species, largely included in the Vipioninae, this number and arrangement persist through all the following instars. The early-instar larvae of the species that develop internally lack the open tracheal system; and, in species that are known to have five instars, the spiracles first appear on the fourth. The species in which only three or four larval instars have been distinguished reveal the spiracles only on the last instar.

De Leon (1934) has summarized the information available regarding the respiratory system of mature braconid larvae and has attempted to group the subfamilies on the basis of spiracle number and position and on the presence or absence of certain commissures. The information available is sufficient for only a very few subfamilies to permit of generalizations in this respect. It appears, however, that the Vipioninae quite consistently have the number and arrangement given above, and limited information indicates that this is true of the Braconinae also. The most common spiracular arrangement, however, has the same number, but the thoracic pair is situated on the second segment rather than the first. This order appears to predominate in the Macrocentrinae, Meteorinae, Euphorinae, Opiinae, and Alysiinae. *Macrocentrus ancylivorus* is said to have the spiracles on the second and third thoracic

and the second to eighth abdominal segments, whereas *M. abdominalis* has 10 pairs, the additional one being upon the ninth abdominal segment. In the Microgasterinae, the occurrence of eight pairs is quite general, and in most species the single thoracic pair is on the second segment, whereas in a smaller number it is upon the third. *Microgaster connexus*, however, has only six abdominal pairs, rather than seven, and *Apanteles lictorius* Rein. is said to have nine pairs, though their position is not given.

On the basis of information regarding a limited number of species, it seems that the greatest variation in spiracle arrangement occurs in the Aphidiinae. *Aphidius granarius* L. has spiracles on the first thoracic and eight abdominal segments, and *Ephedrus plagiator* Nees (Skriptshinskij, 1930) on the second and third thoracic and seven abdominal segments. Wheeler (1923) states that tracheal system and spiracles are absent in the aphidiine species studied, representing three genera but this is so unusual as to require verification.

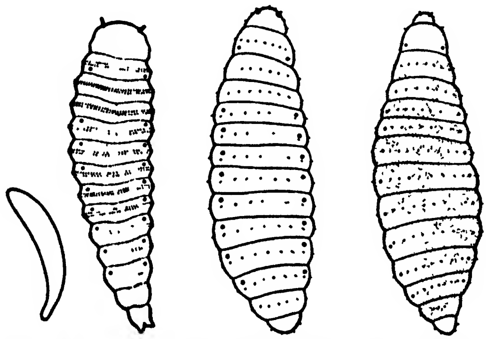


FIG. 22.—The egg and first-, third- and fourth-instar larvae of *Microbracon mellitor* Say. (*From Willard*, 1927.)

The tracheal system of the mature braconid larvae is distinguished from that of the Ichneumonidae chiefly by the absence of the secondary lateral commissures in the thorax, which connect with the main trunks by three branches. The anterior dorsal commissure is present in all species, but the absence of the posterior ventral commissure has been noted in species of *Chelonus*, *Apanteles*, *Microplitis*, and *Meteorus*. Ventral abdominal commissures occur in the first eight segments in several species of Vipioninae and in *Doryctes gallicus* Rh.

Among the species that develop within the host, many have an internal tracheal system but no spiracles in the early instars, and the spiracles appear only in the last larval instar. In *Bracon* sp. (probably *B. hylobii*) studied by Munro (1917), which is the single species of external habit that lacks spiracles in the early instars, they appear first in the fourth (penultimate) instar.

According to Glover (1934), who has studied the immature forms of *B. tachardiae*, the head widths of the five larval instars conform to Dyar's principle, though the extremes overlap, whereas mandible length shows no overlapping.

De Stephani Perez (1902) has described the so-called chrysalid of *Giardinaia urinator* Perez, found upon the stems of *Potamogeton*, which he considers to be the last larval exuviae and within which pupation is said to take place. The last body segment is bifurcate, and the terminal "hooks" are embedded in the stem of the plant. They may bear spiracles, and the supply of air would thus be derived from the plant. The figure of this chrysalid shows 14 segments. The parasite pupa illustrated within it is slightly more than half its length and one-sixth to one-eighth its volume. At emergence, the wasp breaks through the dorsum of the chrysalid and climbs to the surface

of the water. It is extremely improbable that this chrysalid is the last larval skin of *Giardinaia;* it is much more likely to be that of its host. This parasite has been recorded from *Hydrellia* sp. in Europe, and the "chrysalid" described by Perez may be the empty larval skin of a species of Ephydridae. The aquatic larvae of some representatives of this family are known to possess caudal spiracles upon a bifurcate process and to derive their air supply from plants.

EVANIIDAE

This family is represented by a relatively small number of genera and species, all of which are thought to be parasitic in the egg capsules of cockroaches. Earlier authors believed that certain species were parasitic upon the cockroaches themselves, but this habit has not been proved in any instance.

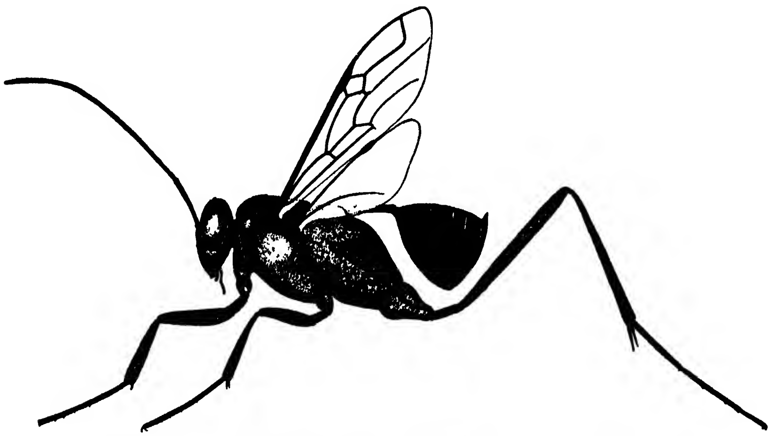


FIG. 23.—The adult female of *Evania appendigaster* L.

Extended biological studies have been made only upon *Zeuxevania splendidula* Costa (Genieys, 1924), which develops in the egg capsules of *Loboptera decepiens* Germ. in Europe. The parasite egg is deposited within one of the eggs in the capsule before the covering is completely hardened. This is in accord with the habit of many other parasites of eggs contained within a capsule or covered with an appreciable quantity of mucilaginous material that hardens quickly. The scelionid parasites of grasshopper and mantid eggs may be cited as further examples of this habit.

The egg is cylindrical in form, 1.0 mm. in length, 0.25 mm. in greatest width, slightly curved, and with one end markedly constricted and terminates in a broadly conical structure which bears a minute pedicel.

The first-instar larva is somewhat cylindrical in form with 13 distinct segments, simple but strongly extruded mandibles, and a complete

internal tracheal system, but no spiracles. In this stage, feeding is confined to the contents of the single egg, but following the first molt the neighboring eggs in the capsule are attacked. In its first stage, the larva is therefore a true egg parasite, whereas it becomes an egg predator after the molt. The second-instar larva is globular in form but otherwise closely resembles the preceding instar, the distinguishing characters being those of the head. The third- and last-instar larva is very robust, about twice as long as wide, with the head large and the mandibles still simple. There are no integumentary spines, sensory setae, or sculpturing upon the body. The tracheal system is now open, with nine pairs of spiracles situated on the first and third thoracic and the first seven abdominal segments. In addition to the usual anterior and posterior commissures, each of the seven abdominal segments possesses an accessory ventral commissure.

Only a single individual is able to develop to maturity in each egg capsule. The winter is passed in the mature larval stage within the capsule, and adult emergence takes place in late spring or early summer.

AULACIDAE

Relatively little is known regarding the habits of this family except that they are mostly parasitic upon larvae of wood-boring Coleoptera, with a few species attacking the larvae of horntail wasps of the family Xiphydriidae. Froggatt records as many as 50 parchment-like cocoons of *Aulacus apicalis* Westw. matted together in the burrow of a larva of *Piesarthrius marginellus* Hope.

STEPHANIDAE

This is a group of exceedingly rare insects, represented by a few genera and species which, so far as the host preferences are known, are parasitic upon the larvae of wood-boring insects.

GASTERUPTIONIDAE

The family is of world-wide distribution and is represented by a considerable number of species; yet little is known regarding its members except that they are parasitic upon solitary wasps and bees. Hoppner (1904) has given a general account of the habits of *Gasteruption assectator* F. as an enemy of *Prosopis* spp. in Europe. The egg is deposited externally upon the body of the mature *Prosopis* larva, though whether this takes place before or after the cell is closed is uncertain. After the host larva has been completely consumed, the *Gasteruption* larva gnaws its way into an adjoining cell and feeds upon a second victim before reaching maturity. The cocoon is formed within the cell of the host.

The mature larva of *G. assectator* is somewhat elongate and bears bands of stout, brownish-colored setae, which are directed caudad, on the dorsum of the segments. A lesser number of these setae occur ventrally. There are nine pairs of spiracles, which are situated on the second thoracic and the first eight abdominal segments. The mandibles are tridentate.

TRIGONALIDAE

The family is a little-known one represented by relatively few genera and species but is of world-wide distribution. It is considered by Wheeler (1923) to be one of the most archaic groups of the Hymenoptera. Some authors consider the family to be most closely allied to the Vespoidea, though its habits and parasitic life link it very closely with the Ichneumonoidea, in which superfamily it is usually placed.

The host preferences of the family as a whole are still obscure. Various species have been reared from the nests of Vespoidea and several from cocoons of ichneumonoid Hymenoptera and from the puparia of Tachinidae. In the case of the Vespidae, the species reared from the nests appear to be primary parasites, whereas those from ichneumonid cocoons and dipterous puparia are hyperparasites, through these hosts, of caterpillars and sawfly larvae. The Australian *Trigonalys maculatus* Smith, on the contrary, is a primary parasite of sawfly larvae of the genus *Perga.*

BIOLOGY AND HABITS

The more detailed biological studies upon the Trigonalidae have been those of Clausen (1929, '31*a*) upon *Poecilogonalos thwaitesii* Westw. and species of several other genera, van der Vecht (1933) upon *Nippogonalos jezoensis* Uch., parasitic in the larvae of *Vespa* spp., and Raff (1934) upon *T. maculatus.* All species, so far as known, are solitary in habit and develop internally in the mature larvae and prepupae of the various hosts previously mentioned. A complete life history, with descriptions of immature stages, is not available for any species, and it has not yet been fully determined, by adequate experiments, in exactly what manner the young larva gains access to its primary host.

The oviposition habits of the family are apparently uniform and have been determined only recently. On the basis of Bugnion's (1910) study of the anatomy of *Pseudogonalos hahni* Spin., which revealed 3,000 to 4,000 minute eggs in the ovaries of each female, Wheeler surmised that oviposition would be found to take place upon foliage and that the first-instar larva would be an active form of the planidium type. The first part of this conjecture has proved to be correct. Leaf oviposition in this family was first observed by Teranishi (1929) in the case of *Poecilogonalos maga* Tera., and a similar habit has since been noted by other

investigators in *P. thwaitesii*, *P. henicospili* Roh., *Orthogonalos debilis* Tera., *Nippogonalos jezoensis* Uch., and *Pseudogonalos* sp. In all species, the female stands upon the upper surface of the leaf, curls the tip of the abdomen beneath the margin, and deposits the egg on the lower surface at a distance of 0.5 to 1.0 mm. from the edge (Fig. 25). In *N. jezoensis*, a modification of this habit has been noted by van der Vecht; the eggs are placed singly in minute incisions in the leaf tissue but near the margin, and the leaf tissue is damaged on both sides. They are placed in the foliage of a wide variety of plants and, in some instances, in the petals of the blossoms, also.

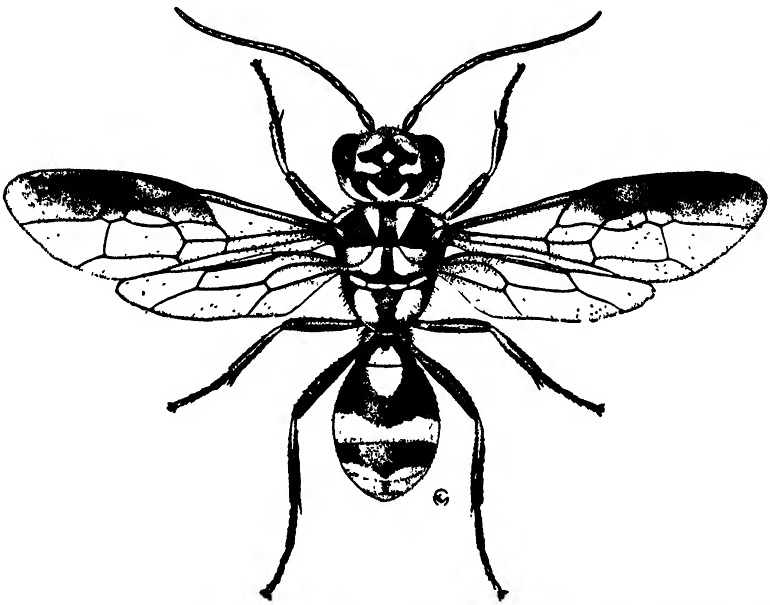


FIG. 24.—The adult female of *Poecilogonalos thwaitesii* Westw. (*From Clausen*, 1929.)

Under field conditions in a given locality, the eggs of a particular species are usually deposited upon a single species of plant, though in another locality the plant chosen may be an entirely different one. Experiments indicate that the physical qualities of the leaves have a direct bearing upon the readiness with which the females oviposit upon different plants but that the principal influence may possibly be the occurrence of the caterpillar or sawfly host upon the foliage. There is as yet no direct evidence to indicate that the latter is true, and caged females oviposit quite as readily upon clean foliage as upon that on which caterpillars are present or on which they had previously fed.

The oviposition capacity of female Trigonalidae is exceedingly high, as was pointed out by Bugnion. Actual oviposition records show the

deposition of 3,559 eggs in 4 days by a female *P. maga*, while 10,641 were secured from a single *P. thwaitesii* female in 14 days and 5,782 in 6 days from *P. henicospili*. The *P. thwaitesii* individual referred to deposited 4,376 eggs in a single day. This exceedingly high reproductive capacity is essential in view of the mortality factors that operate prior to the time the primary host is reached.

It had been found by Clausen that the microtype eggs of the Trigonalidae consistently fail to hatch when left upon the foliage, though eggs

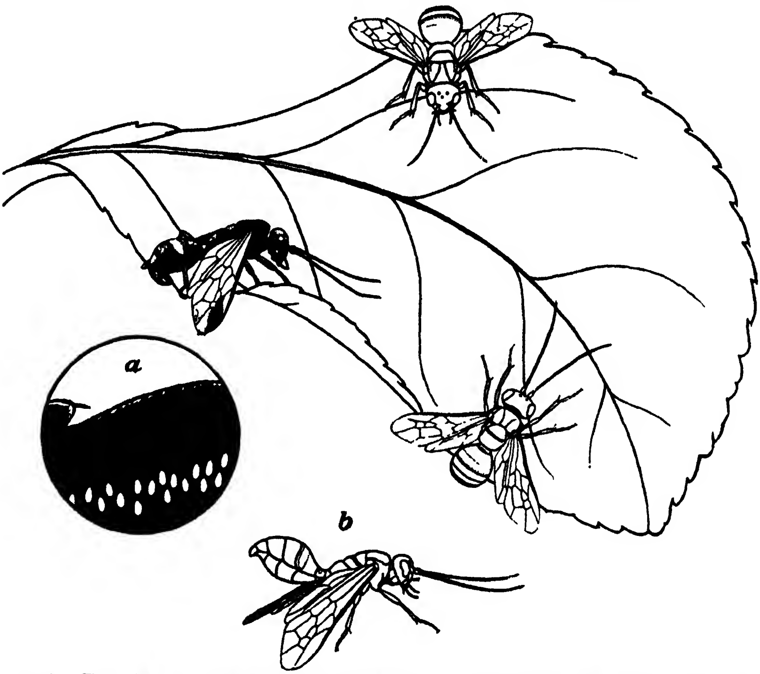


Fig. 25.—Females of *Poecilogonalos maga* Tera. ovipositing beneath a leaf margin; (*a*) a group of eggs, much enlarged and (*b*) a female in the characteristic resting position. (*From Clausen*, 1931.)

several months old were determined still to contain viable larvae. Experiments with chemicals, such as a weak solution of potassium hydroxide, induced emergence provided that the chorion was first ruptured. This led to the supposition that the eggs must be eaten by the host in order to secure normal hatching, a condition already known to be obligatory in several species of Tachinidae. Tests with lepidopterous larvae proved this to be the case, and hatching results from the cracking of the chorion by the mandibles of the caterpillar followed by the stimulating effect of the digestive juices. The larvae are found free in the alimentary tract one to six hours after ingestion of the eggs by the caterpillar and shortly thereafter they enter the body cavity. Several first-instar larvae

of *P. maga* were found within the body of a sawfly larva collected in an area where the species was known to occur, thus verifying the conclusions arrived at experimentally.

According to van der Vecht, the larger larvae of *Vespa velutina* Lep. and *V. analis* F., which are the hosts of *N. jezoensis*, are fed mainly, if not exclusively, with fragments of bees, flies, ants, etc., and there is thus no direct clue as to the means by which the *Nippogonalos* larva reaches its host.

The first- to third-instar larvae develop internally in the body of the host, and the surplus individuals are eliminated in the third stage. The mandibulate third-instar larvae show a marked cannibalistic tendency. Just prior to issuance, the parasite larva assumes a position immediately beneath the derm of the thorax, with the head embedded in an eye of the developing host pupa, and emergence of the fourth-instar larva always occurs at this point. Emergence from the host prepupa or pupa is accomplished immediately after the third molt of the parasite, and death of the host occurs at this time. Feeding then takes place externally until the fourth molt. In spite of its heavy tridentate mandibles, the fifth-instar larva feeds very little; only a portion of the fluid contents of the host body is sucked out, and no solid tissue is eaten.

The mature larva spins its irregular cocoon within that of the host, and partitions off the meconium of the host and its putrefying remains. According to Raff, *Trigonalys maculatus* spins no cocoon whatever, though a transverse partition, of host origin, in the *Perga* cocoon separates the pupa from the exuviae of the sawfly host, and the prepupal remains of the latter are within the cell occupied by the *Trigonalys* pupa. Van der Vecht states that the larva of *Nippogonalos* emerges from the body of its *Vespa* host after the latter has closed its cell preparatory to pupation and that the mature parasite larva, after completing its feeding externally, makes a cross-wall of silk at the middle of the *Vespa* cell, thus isolating the host remains in the lower portion. This lower compartment is apparently opened and cleaned by the *Vespa* workers, and the parasite adult later emerges through a hole made in the cross-wall.

The life cycle has not been definitely ascertained for any species; but evidence points to a general one-year cycle in the temperate regions, whereas in tropical regions it must be longer than that of the host, for the duration egg stage is exceedingly variable and may extend over several months. Development of the early-stage larva is then delayed until the host approaches the prepupal stage.

The developmental cycle of members of the family upon the three groups of hosts from which they have been reared is outlined below. That given for the Vespoidea is hypothetical but appears to be the only logical means by which the larval host can be reached.

Trigonalid female

Eggs deposited upon foliage

Eggs eaten by caterpillars or sawfly larvae

Secondary host parasitized by ichneumonoid (before or after eggs have been eaten)	Larvae eaten by adult vespoid wasp	Secondary host parasitized by tachinid (before or after eggs have been eaten)
Trigonalid larva enters body of ichneumonoid larva	Body fluids of larvae, containing first-instar trigonalid larvae, fed to vespoid larvae	Trigonalid larva enters body of tachinid larva
Development within ichneumonoid larva	Development within vespoid larva	Development within tachinid larva
Adult emerges from ichneumonoid cocoon	Adult emerges from vespoid cell	Adult emerges from tachinid puparium

IMMATURE STAGES

The microtype egg of *P. thwaitesii* (Fig. 26A) measures 0.12 by 0.07 mm., is ovoid in form, flat ventrally, and arched dorsally, and bears a series of five to seven longitudinal ridges on the dorsum. The chorion is exceedingly hard and translucent. Other species observed have eggs of similar form, with slight variations in size and in the number and prominence of the longitudinal ridges. Those of *N. jezoensis* are said to be convex on both sides.

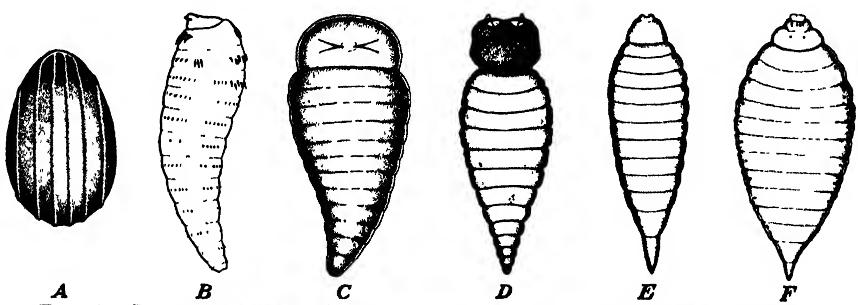


FIG. 26.—Immature stages of the Trigonalidae. *A*, the microtype egg of *Poecilogonalos thwaitesii* Westw.; *B*, the microtype first-instar larva of *P. maga* Tera.; *C*, *D*, *E*, and *F*, second- to fifth-instar larvae of *P. thwaitesii*. (*From Clausen*, 1929, 1931.)

The microtype first-instar larvae have been described only for *P. maga* (Fig. 26*B*) and *Orthogonalos debilis* (Clausen, 1931), and these are very similar in form. They are 0.12 mm. in length, with 12 body segments, broadest in the thoracic region and tapering gradually caudad. The head is broad, largely retracted into the thorax and the mandibles are slender and extruded. The first thoracic segment has a transverse

ventral row of five exceedingly heavy hooks, directed caudad, and a heavily sclerotized palmate plate dorsally on the median line. The second and third segments have the row of heavy spines both dorsally and ventrally. Each abdominal segment has a transverse row of minute setae both ventrally and dorsally, those on the last two or three segments forming a complete ring.

The intermediate-larval instars have been described for *P. thwaitesii* only, and these were secured by dissection of parasitized *Henicospilus* larvae taken from their cocoons. The second instar (Fig. 26*C*) is markedly different from the first, having a large hemispherical head, with large but lightly indurated mandibles, and 12 body segments which bear no hooks or setae. The third instar (Fig. 26*D*) is of the mandibulate type similar to the first instar of many other Ichneumonoidea. It has a single pair of spiracles at the anterior margin of the second thoracic segment. The fourth-instar larva (Fig. 26*E*) is more slender, with the head of normal form, and the caudal segments are somewhat attenuated. There are eight pairs of spiracles, situated on the second and third thoracic and the first six abdominal segments, of which the first pair is much the largest. The fifth-instar larva (Fig. 25*F*) is very robust in form and bears no integumentary spines or setae. The spiracles are as in the preceding instar. The mandibles are tridentate as compared with the simple form of those of the preceding instars.

ICHNEUMONIDAE

This is an exceedingly large family, in so far as the number of species is concerned, and the adults vary greatly in size, form, and coloration. It comprises some of the most conspicuous forms among the parasitic Hymenoptera, notable among which are the species of *Rhyssa* and *Megarhyssa* of the tribe Rhyssini. The members of this group are parasitic upon the larger wood-boring Hymenoptera and are conspicuous because of the extreme length of the ovipositor. The female of one unnamed ichneumonid species from Peru which is figured by Bischoff (1927) has this organ 15.0 cm. in length as compared with a body length of only 2.0 cm.

Although the great majority of species have fully developed wings and are very active in flight, some species, particularly of the cryptine genus *Gelis*, have apterous females and the males may be either winged or apterous. Muesebeck and Dohanian (1927) state that the males of *G. apantelis* Cush., *G. nocuus* Cush., and *G. inutilis* Cush. are always winged, whereas both forms are found in *G. urbanus* Brues and *G. bucculatricis* Ashm. There is no regularity in the appearance of either form, and both are produced by virgin as well as mated females. According to Thompson (1923*a*), intermediate forms, with the wings in various stages of reduction, are known in *G. sericeus* Foerst. The production of both winged and apterous individuals of the same sex is considered to be due probably to a difference in the quantity of food material available to the individual larvae. In *Hemiteles hemipterus* F., both sexes of which are alate, there is a marked variation in wing size among the females, some having wings only half as long as others, and with a modified venation.

In the practice of biological control of plant pests, ichneumonid parasites have been imported into a number of countries and colonized in infestations of various lepidopterous and other pests. Rather surprisingly, however, the results have not been so satisfactory as with several other parasitic groups, and only two instances are known where pronounced benefit was secured. *Bathyplectes curculionis* Thoms., imported from Italy, has contributed materially to the control of the alfalfa weevil, *Hypera variabilis* L., in the United States; and *Mesoleius tenthredinis* Morley, imported into Canada from England, is credited with a large part in the control of the larch sawfly, *Lygaeonematus erichsoni* Htg.

HOST PREFERENCES

The great majority of species of this family are primary parasites and many exert a pronounced effect upon the host population. Because of the large number that have been studied and the great range in host preferences, the principal subfamilies will be discussed separately, with particular reference to the principal tribes and genera where a uniformity of preference is shown within these lower groups.

The species of the subfamily Joppinae are consistent in their host preferences and are recorded only as internal parasites of the larvae and pupae of Lepidoptera. In the species attacking the larva, emergence of the adult is from the pupa. The dominant genus is *Amblyteles*, which is of world-wide distribution and is represented by a very large number of species.

The Cryptinae are external parasites of a very wide range of host groups, though the tribe Cryptini contains many species that are internal parasites.

In the role of primary parasites, the members of the subfamily attack lepidopterous larvae most frequently, though a few species are known to develop upon sawfly and coleopterous larvae, and an occasional species upon the pupae of Trichoptera and Diptera. Many species of the genus *Gelis* (*Pezomachus*) are predaceous upon the eggs and young spiders in the egg sacs. In *Hemiteles hemipterus*, the habits of which have been studied by Salt (1931*b*), there appears to be an obligatory alternation of generations. The females reared from larvae of the wheat stem sawfly, *Cephus pygmaeus* L. during May and early June refuse to oviposit in this host but readily accept others. Under field conditions, *Cephus* larvae are not available until the end of August, so that there is ample time for the development of a midsummer brood upon some host as yet unknown. The autumn brood of *Xylophruridea agrili* Vier. develops upon the mature larvae of *Agrilus*, whereas the spring brood attacks the pupae of the same host species.

Habrocryptus graenicheri Vier. (Graenicher, 1905*a*), which develops at the expense of the egg and larval instars of *Ceratina dupla* Say, is of unusual habit in that the host stages contained in three or four cells may constitute the food of a single larva.

There is a strong tendency toward the hyperparasitic habit in this subfamily. Many species of *Gelis* attack the larvae in the exposed cocoons of various Braconidae, particularly the Microgasterinae, and in those of other Ichneumonidae. The genus *Hemiteles* also contains many species that are either obligate secondary parasites or are able to develop in either the primary or the secondary role. *H. hemipterus*, already mentioned, may possibly develop in the latter capacity in its midsummer generation. According to Faure (1926), the larvae of *Spilocryptus ferrieri* Faure and a variety of *S. migrator* F. are predaceous upon those of *Pteromalus variabilis* Ratz. in the pupae of the cabbage butterfly.

The Ichneumoninae are a large group having varied host preferences, though the greater number of species probably are internal or external parasites of lepidopterous, coleopterous, and hymenopterous larvae, particularly the wood- and stem-boring forms, and a considerable number attack lepidopterous pupae. Many of the species of the Ephialtini are distinguished by an exceptionally wide host range, some attacking a large number of Lepidoptera and also including Coleoptera and Hymenoptera among their hosts. The most frequently encountered genera of the subfamily are *Lissonota, Glypta, Ephialtes, Scambus*, etc. The members of the Rhyssini are external parasites of hymenopterous larvae of the phytophagous families Xiphidriidae and Siricidae. Records of members of this tribe attacking coleopterous larvae are open to question. A considerable number of species are external parasites of spiders, and the genus *Polysphincta* is known to be limited to such hosts. *Tromatobia* and *Zaglyptus* develop as predators in spider egg sacs, though *Z. variipes* Grav. is reported (Maneval, 1936) to develop as a parasite of the adult spiders themselves. Nielsen (1935) mentions that the larvae of this species not only suck out the fluid contents of the dead spiders but consistently feed also upon the eggs in the nest.

Species of the genera *Grotea, Macrogrotea*, and *Echthropsis* develop at the expense of bees and have the habit of destroying the egg or young larva in the cell and then completing their feeding upon the beebread with which the cell is provisioned.

The members of the subfamily Tryphoninae are predominantly solitary parasites of the larvae of sawflies, though a few species attack lepidopterous larvae and pupae and dipterous larvae. The sawfly parasites are contained in the tribes Catoglyptini, Ctenescini, and Tryphonini, whereas those attacking caterpillars are largely in the

Paniscini, of which the most frequently encountered genus is *Paniscus*. The species of the genus *Sphecophaga*, of the first-named tribe, are parasitic in the larvae and pupae of *Vespa*. The Ctenescini, Tryphonini, and Paniscini are external parasites. The Diplazonini, represented principally by *Diplazon*, *Syrphoctonus*, and *Homotropus*, are internal parasites of Diptera, particularly the Syrphidae, and the less common Exochini and Metopiini develop internally in lepidopterous pupae. *Hypamblys albopictus* Grav. is an internal parasite of *Nematus* larvae, and *Oocenteter tomostethi* Cush. develops similarly in larvae of *Tomostethus*.

The Ophioninae are recorded as internal parasites only, and the great majority of species, included mainly in the tribes Ophionini, Campo-

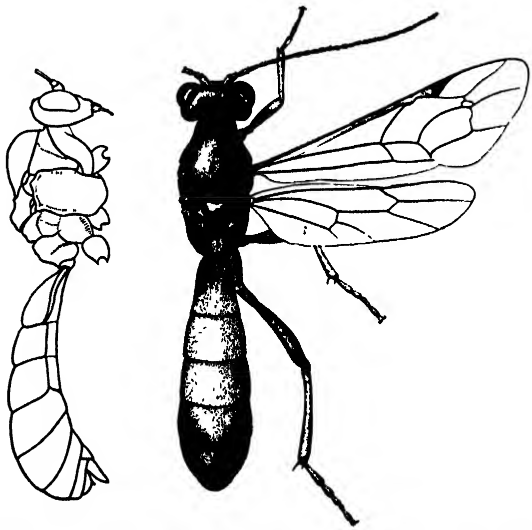


FIG. 27.—The adult female of *Tryphon incestus* Holmg. (*From Clausen*, 1932.)

plegini, and Cremastini, develop at the expense of lepidopterous larvae. In the Ophionini, however, several species of *Ophion* are known to depart from the general habit of the group and are internal parasites of scarabaeid grubs in the soil. The species of the genus *Bathyplectes*, of the Campoplegini, are apparently limited to curculionid larvae, whereas *Holocremnus* and *Olesicampe* attack sawfly larvae. Most of the Therionini and Banchini attack lepidopterous pupae. The Porizonini are of varied habit, with *Orthopelma* parasitic in cynipoid larvae and *Thersilochus* in those of certain Curculionidae. The hyperparasitic habit is strongly developed in the Mesochorini, of which the most frequently encountered genus *Mesochorus* attacks the larvae of Braconidae and of other Ichneumonidae.

BIOLOGY AND HABITS

The biology and habits of the Ichneumonidae present a number of features of particular interest; and, because of the abundance of species, their wide distribution, and their importance in the natural control of many of our leading crop pests, they have been extensively studied and a large mass of published data is available regarding them. Cushman (1926*b*) has given an account of the principal types of parasitism found in the family, with illustrations of the various modifications in the egg and larval forms. He distinguishes four types of external parasitism, of which the first, exemplified by the Rhyssini and Ichneumonini, is the least specialized and much the most common. The egg is simple in form and is deposited upon or near the host, which is enclosed in a cocoon, feeding burrow, or pupal shell or is otherwise enveloped. The host may be permanently paralyzed or killed by the sting of the parasite, or it may not be stung at all.

The second type includes the Polysphinctini parasitic upon spiders, in which the host is temporarily paralyzed and the firmly fixed eggshell is utilized by the developing larva as a means of maintaining its attachment to the host body. The third type is somewhat similar to the second, but the egg is provided with a pedicel which is inserted through a puncture in the skin of the host. The species of Paniscini and Tryphonini and the recently discovered Lysiognathinae are of this type, and attack is upon free-living caterpillars and sawfly larvae.

The fourth type, revealed in *Grotea* and related genera, differs from the first in that the egg or young larva of the bee host is first consumed and further development is upon the plant materials with which the cell is provisioned.

Cushman further distinguishes five types of internal parasitism which, however, are not nearly so well defined as the external forms. These represent a progressive specialization, principally in larval forms and habits; but the host relationships of this enormous family are still much too incompletely known to permit of anything more than a tentative arrangement.

There is a considerable variation in the reproductive systems of the females of the several groups of the family in consequence of the different types of eggs deposited and the manner and place of oviposition. Pampel (1914) has given a very extended and well-illustrated account of the female reproductive organs and the eggs of a large series of species, representing all the principal subfamilies, and he finds that they are of four distinct types. The most highly specialized of these is designated the ***Tryphon*** type, illustrated by the Tryphoninae, in which uterine incubation may take place and the egg is equipped with a pedicel that

permits of its being carried on the ovipositor and partially embedded in the skin of the host when deposited. Among the species of Tachinidae that incubate the eggs before deposition, the posterior uterus is thick-walled and abundantly provided with tracheae, forming a distinct incubating organ; but such an adaptation appears to be lacking in the Tryphoninae, and it may be unnecessary in view of the very small number of eggs that can be contained in the uterus at any one time.

The *Ophion* type of reproductive apparatus is somewhat similar to the above; but the number of ovarioles is large, totaling 30 to 80, and the eggs are proportionately smaller. The oviducts are often much longer than the ovaries themselves.

In the borer type, represented by *Ephialtes* and *Rhyssa*, the number of ovarioles is only 8 to 12, and these are very long and the stalked eggs, of which there are only two or three in each, extend almost the entire length. The ovipositor is very slender, to permit of penetration of bark, etc., and the stalked form of the egg allows it to pass through a very narrow channel.

The *Ichneumon* type of reproductive apparatus consists of a small number of long ovarioles, each containing three or four eggs, of which only one is mature, and only the basal third of each ovariole contains eggs. The oviduct is short and the uterus short and flattened. The mature eggs are large and unstalked.

Habits of the Adult.—The preoviposition period has been determined for only a few species and appears to be rather variable. *Nemeritis canescens* Grav. is reported to be able to deposit eggs the day of adult emergence (Daviault, 1930), whereas *Glypta rufiscutellaris* Cress. does so in 2 to 6 days (Crawford, 1933) and *Exeristes roborator* F. in 5 to 10 days (Fox, 1927). In *Ephialtes extensor* Tasch. (Rosenberg, 1934), the period elapsing between emergence and first oviposition is 10 to 19 days at 25°C. and 20 to 30 days at outdoor temperatures during the early part of the year. Cushman (1913*b*), dealing presumably with this species (given as *Calliephialtes* sp.), mentions a gestation period of about 9 days. *Phaeogenes nigridens* Wesm. requires about 11 days at 25°C., but this period is greatly extended at lower temperatures, being approximately one month at 18°C. and three months at 8°C.

The length of adult life in the majority of species for which this is known covers approximately six to eight weeks, the period thus being appreciably longer than in the Braconidae. Those which hibernate in the adult stage naturally are adapted for a long life, and adults of *P. nigridens* have been kept alive as long as 10 months under insectary conditions.

The stimuli that induce oviposition by the female are varied and are related more or less directly to the habits of the host stages attacked.

In free-living larvae, the host body itself provides thė stimulus; but where larvae or pupae in tunnels or cocoons are attacked preliminary direct contact is not possible. In *Pimpla instigator* F., odor seems to be the inciting agency, and great activity by the females is induced by fresh host blood (Picard, 1921). Actual deposition of the egg, however, requires tactile responses through organs on the ovipositor. In host stages contained in a cocoon, it is often the cocoon itself that provides the stimulus, whereas with larvae boring in stems, fruit, etc., it is frequently the frass that accumulates at the entrance to the burrow. The majority of species that parasitize protected host stages will show no interest in them when they are removed from the cocoon or tunnel. In the case of *Spilocryptus extrematis* Cress. the Cecropia cocoon appears to provide the necessary stimulus, for free larvae are never attacked (Marsh, 1937). Females are attracted in large numbers as soon as the larvae begin spinning, and this very evidently is an odor response. In one instance, 34 females were seen ovipositing in a single cocoon at the same time, and a total of 1,011 eggs was later found in it. Cushman (1916) found that the oviposition scar of *Conotrachelus* apparently provides the necessary stimulus for *Thersilochus conotracheli* Riley, and he observed that females would often attempt to insert their ovipositors in abrasions in the skin of plum fruits, whether or not they were infested with curculio larvae.

FIG. 28.—A female of *Calliephialtes* sp. stinging a codling-moth larva preparatory to oviposition. (*From Cushman,* 1913.)

Probably a majority of the members of this family oviposit directly on or in the host stage upon which the larva is to complete its development, though many attack the host in its larval stage and emerge from the pupa. The first record of an ichneumonid species ovipositing in the egg of its host is that by Kurdjumov in 1915, who found that *Collyria calcitrator* Grav. does so but does not complete its larval development until the host larva is nearly mature. More recently Cushman (1935) has shown that *Oocenteter tomostethi* places its egg in that of the sawfly host and the latter attains larval maturity and spins its cocoon before death. *Sagaritis dubitatus* Cress. has been reported to place its egg in

the host embryo immediately before hatching, but other investigators question this observation and state that oviposition is only in late first- or early second-instar armyworms.

The oviposition habits of *Diplazon laetatorius* F., particularly as they pertain to the stage of the syrphid host attacked, are of special interest. The egg may be placed in either the egg or the larva, and the adult parasite emerges from the puparium. Kelly (1914*b*) observed oviposition in eggs of *Baccha* in 1909 and secured the adults from the puparia of those individuals. Later investigators have found that oviposition takes place in eggs only when the embryo is fully developed and that young larvae are also attacked. Kamal (1939) states that the first and second larval instars are preferred for oviposition. In *D. tetragonus* Thbg., on the other hand, it is reported by Bhatia (1938) that oviposition is only in third-instar larvae.

The eggs of larval parasites that oviposit in the eggs of the host are usually of minute size, but *Diplazon* is a conspicuous exception to this rule. That of a species observed in Japan, which has been listed as *D. laetatorius* F., measures 0.65 mm. in length and 0.14 mm. in width and is forced into a syrphid egg only 1.0 mm. in length and 0.35 mm. in width. The distention of the host egg thus produced is often so great as to break the waxy incrustation that covers it, and it is surprising that the host embryo is able to complete its development and the larva to hatch normally with so large an egg within its body.

The great majority of species of Ichneumonidae that develop internally in the host place the egg more or less at random in the body cavity, though the eggs have a tendency to move with the blood stream and they frequently lodge at the posterior end of the abdomen. *Heteropelma calcator* Wesm., however, inserts the ovipositor through the mouth or the anal opening, and the egg is fixed to the thin lining of the terminal portions of the alimentary canal. Only in *Amblyteles subfuscus* Cress. is the egg position known to be confined to a single organ, and in this instance it is always in the salivary gland (Strickland, 1923).

The external parasites which attack larvae in cocoons, galleries or leaf-rolls place the egg upon any part of the body of the host or loosely near by. That of *Grotea anguina* Cress. is placed longitudinally upon the egg of the host in the cell. The female of *Pimpla macrocerus* Spin., which attacks the mature larva of *Odynerus* in its hard-walled cell, secretes a drop of fluid at the tip of the ovipositor, which serves to soften the wall and thus facilitates penetration (Janvier, 1933). The egg is attached to the interior of the wall of the cell, and at hatching the young larva drops to the body of the host.

The bulk of the species of the Tryphonini and Paniscini are of unusual habit in that they attack free-living larvae which continue their feeding

after being parasitized. The species of *Paniscus* and *Phytodietus* that have been studied place the egg in an intersegmental groove between two thoracic segments or between the thorax and the abdomen. *Tryphon incestus* invariably inserts the pedicel of the egg in the neck of the host larva (Fig. 33*B*), either dorsally or laterally, whereas *Lysiognatha* appears to attach it most frequently to the head. Several other species of this subfamily attach the eggs at the side of the body, usually on the thorax or anterior abdominal segments, but *Exenterus coreensis* Uch. consistently places it transversely on the median dorsal line of the second thoracic segment.

The majority of species of *Polysphincta* and other genera of spider parasites place the egg dorsally or laterally at the base of the spider abdomen, though a few are recorded as depositing it on the posterior declivity of the cephalothorax. The latter is the normal habit of *Schizopyga podagrica* Grav. The female of *Zaglyptus variipes*, on the other hand, kills the female spider in her nest and then deposits from one to eight eggs upon the freshly formed egg "cocoon" (Nielsen, 1935).

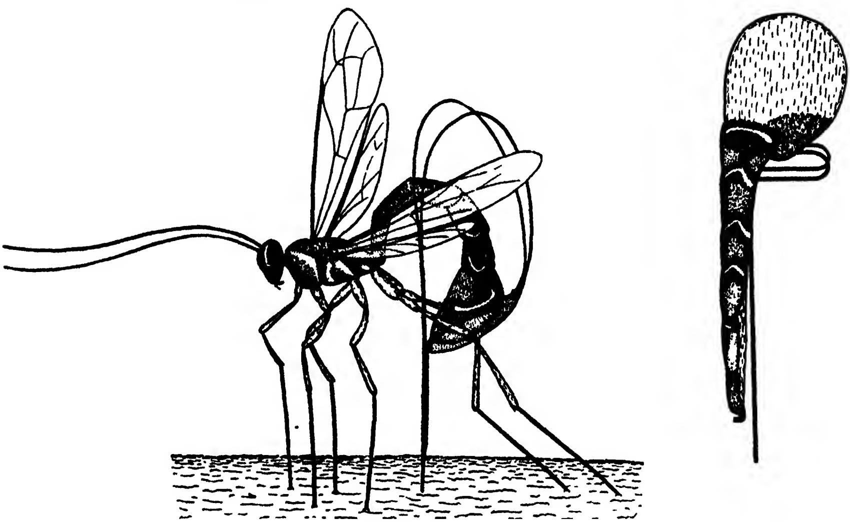
The species of *Mesochorus* which develop in braconid and ichneumonid larvae are indirect in their relationship, for oviposition takes place in the body of the primary host while the latter is still contained in the living caterpillar. A similar habit is recorded for *Stictopisthus javensis* Ferr., which attacks *Euphorus* larvae in *Helopeltis* in Java.

Oviposition by the ectoparasitic Tryphoninae is different in several respects from that by other groups of similar habit. Even though free-living larvae of considerable size are attacked, yet many species do not even momentarily paralyze them. Several species of *Paniscus*, however, accomplish this by an insertion of the sting in the thoracic region prior to that which results in egg deposition. The female of *Tryphon incestus* springs upon the sawfly host from the rear and inserts the egg pedicel in the neck by a lightning-like thrust of the ovipositor. Chewyreuv (1912) has described in detail the manner of oviposition of two species of *Paniscus;* he observed that some eggs were deposited upon host caterpillars which were still active, whereas others were upon completely, though temporarily, paralyzed individuals.

In all the species having the pedicellate type of egg, only the pedicel or anchor is held within the channel of the ovipositor, and the main body issues ventrally at the base of the ovipositor immediately after it leaves the oviduct. Because of its large size and heavy, inelastic chorion, the egg could not be compressed sufficiently to permit of its passage through the channel of the ovipositor.

The manner of oviposition of the species attacking wood-boring larvae has attracted much attention, not only because of the considerable depth of wood through which the ovipositor must penetrate, but also because

of the extreme length of this organ in some species, which necessitates an involved process of manipulation to attain the required position for drilling and to exert the force necessary for penetration. Riley (1888) has given an extended account of the manner of oviposition of *Megarhyssa lunator* F. (Fig. 29); in this species, the hind legs are used to bring the ovipositor into a vertical position. The sheaths of *Megarhyssa* are arched dorsally over the abdomen and serve to guide the ovipositor proper, but they do not penetrate the wood. In the early phases of the act, the forcing of the basal portion of the ovipositor into a coil in a membranous intersegmental "sac" between two of the abdominal



A **B**

FIG. 29.—Oviposition by *Megarhyssa lunator* F. *A*, the female with the ovipositor in position; *B*, the abdomen in the vertical position assumed in order to bring the tip of the ovipositor forward beneath the body; At this stage the basal portion of the ovipositor is coiled within the abdomen at the periphery of the membranous distention between the sixth and seventh segments. (*Redrawn, after Riley*, 1888.)

segments permits of the terminal portion being brought into a perpendicular position for the beginning of drilling. This provision for manipulating an ovipositor of exceptional length is also found in *Leucospis* of the Chalcidoidea. Abbott's more recent account (1934) describes and figures in detail the mechanics of oviposition. Cheeseman (1922) describes the oviposition of *Rhyssa persuasoria* L., and Brocher (1926) discusses the manner in which it is accomplished by *Perithous mediator* Grav.

Several authors have asserted that *Megarhyssa* drills at times through solid wood to reach the host for oviposition, but this is questioned by Abbott, who finds that cracks, crevices, etc., are utilized to reach the host burrow and that the only real drilling which takes place is through the

bark. The parasite may possibly utilize the oviposition holes previously made by *Tremex*. Chrystal and Myers, however, assert that *R. persuasoria* can and does at times penetrate solid wood.

An interesting point is brought out by Rosenberg with respect to oviposition by *Ephialtes extensor*. The eggs that are deposited during the latter portion of the oviposition period of the female are consistently of different form from the ones first laid, being markedly wider in relation to the length. A portion of the eggs of this species are devoid of contents when laid, and the number of these is greater after a period of rapid oviposition and during the latter portion of the oviposition period of the female.

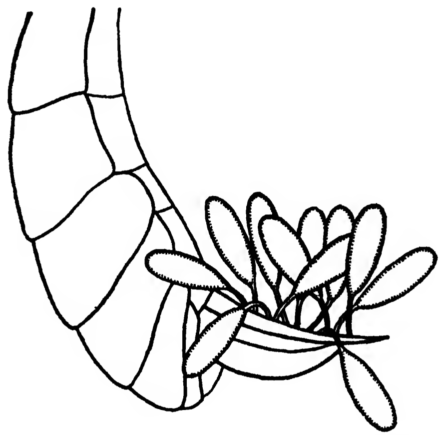


FIG. 30.—The abdomen of a *Tryphon* female, lateral view, showing a cluster of eggs carried upon the ovipositor. This habit is common to several genera of the Tryphoninae.

Chewyreuv (1912) has called attention to the habit of the females of many Ichneumonidae of dropping their eggs at random in case hosts are not available. This is true more particularly among the ectoparasitic species and is stated to be due to the necessity of eliminating the mature eggs in the oviduct to make way for others that have been developed, and also to avoid injury to the internal organs of the parent. Such action is disadvantageous to the parasite, for it involves the loss of these eggs. It has been noted by H. D. Smith (1932) that no eggs are ever found in the oviduct of *Phaeogenes nigridens* Wesm. and that those which mature in the folicles soon disintegrate and pass out through the oviduct if there is no opportunity for oviposition.

In a number of species of Tryphoninae, the mature eggs are conserved, for a time at least, by being carried externally upon the ovipositor, with only the pedicel held between the blades (Fig. 30). This habit appears to be quite general in *Polyblastus* and has been observed also in *Dyspetes* and *Tryphon*. Pampel mentions one female of *P. cothurnatus* Grav. carrying 17 eggs upon the ovipositor, and *T. incestus* Holmg. has been observed to carry as many as 10. These eggs are of large size, and in both cases the number carried was in excess of that which could be accommodated in the uterus. The occurrence of this habit is not correlated with the stage of incubation of the egg, nor is it obligatory. In the case of *T. incestus*, it was concluded that the presence of eggs upon the ovipositor was only accidental, the result of unsuccessful attempts at

oviposition, in which the act was interrupted between extrusion of the egg and its attachment to the host larva. The eggs thus carried on the ovipositor may eventually be discarded, or they may be utilized in later successful oviposition.

Kerrich (1936), in discussing the retention of eggs on the ovipositor by *Polyblastus strobilator* Thbg., came to the conclusion that this is a provision for protection of the progeny. There is little evidence, however, that this habit is of any advantage to the parasite other than in conserving the eggs during a period when, for any reason, normal oviposition is not possible.

The adult females of a great many species of Ichneumonidae feed upon the body fluids of the host stages that they parasitize; this is either incident to oviposition or entirely independent of it. This habit is most general in the Ichneumoninae and the Cryptinae. *Polysphincta parva* Cress. feeds upon the body fluids that exude from ovipositor punctures in the body of the spider host (Cushman, 1926). In *Ephialtes*, *Exeristes*, and related genera, the feeding may have no relation to oviposition, and the punctures are often enlarged by use of the mandibles. Not only the fluids but the entire body contents may be consumed; and the feeding habit, instead of being incidental to and associated with oviposition, has developed into a distinctly predaceous habit, independent of the reproductive activities, though very probably essential to oögenesis. *Pimpla instigator*, *Itoplectis conquisitor* Say, and several species of the cryptine genus *Hemiteles* have the habit of feeding, while the ovipositor is still inserted, upon the host body fluids that rise along the ovipositor by capillary action. *H. hemipterus* feeds upon the fluids of codling-moth larvae, though reproduction takes place only as a secondary parasite, through *Ephialtes*. *Diplazon laetatorius*, which oviposits either in the syrphid egg or young larva, makes an initial insertion of the ovipositor in the egg for exploratory purposes and then applies the mouth parts to the puncture. If the embryo is well developed, the ovipositor is reinserted and the egg laid, but if the egg is still quite fresh the contents are completely sucked out. The number thus consumed may be vastly greater than is utilized for oviposition. No representative of the family is known to construct a feeding tube such as is made by many Braconidae and Chalcidoidea.

In those species of the family that attack larvae in cocoons, tunnels, leaf rolls, etc., and whose larvae feed externally, the host is usually permanently paralyzed at the time of oviposition. This habit is most general in the Ichneumoninae and Cryptinae. The codling-moth larvae stung by *Aenoplex carpocapsae* Cush. are stated by McClure to remain in a fresh physical condition for a maximum of 73 days and an average of 26 days. *Spilocryptus extrematis* kills the Cecropia larva at the time

of oviposition, and the substance injected into the body at the time of stinging exerts a pronounced preservative effect. The larva of *Gyrinus*, which is the host of *Hemiteles hungerfordi* Cush., is stung by the parasite but is not paralyzed, though it is stated that further development is inhibited. In a number of species, particularly of the genus *Exeristes*, the host larva is often killed by the sting, and a repetition of stinging frequently results in death of the host in the case of species that normally effect only permanent paralysis. The female of *Phaeogenes nigridens* enters the corn-borer tunnel in search of its host, bites away an opening in the cocoon, enters it and then stings the pupa at the base of one of the wing pads.

Polysphincta paralyzes its spider host only temporarily, and *P. eximia* Schm. is said to insert its sting in the mouth. In this genus, it is probable that the paralyzing agent injected at the time of stinging, rather than the feeding activities of the young larva, is responsible for the inhibition of molting by the host.

Egg and Larval Development.—With the great majority of species, except those of the Tryphoninae, the period of incubation of the egg is relatively short, ranging from one to three days. A number of species are stated to require six to eight days, but in some of these, at least, the longer period has been due to low temperatures prevailing during the period the eggs were under observation. In several species that deposit their eggs internally, it has been observed that there is an appreciable increase in size during incubation, though this is not nearly so general nor is the growth so extensive as in the Braconidae.

The greatest variation in habit relating to egg production and incubation is found among the Tryphoninae. Of the endoparasitic species, *D. laetatorius* hatches in 1 to 4 days, and *Hypamblys albopictus* is reported to require the exceptionally long period of about 14 days. Among the ectoparasitic forms, there are found the only instances of uterine incubation known among the parasitic Hymenoptera, which is in contrast with its frequent occurrence in the parasitic Diptera. This habit is normal in some, though not all, species of *Paniscus*, *Polyblastus*, and *Dyspetes*. Complete uterine incubation is apparently normal in *Paniscus cristatus* and *P. ocellaris* Thoms., as judged by the results of dissections reported by Chewyreuv, and several instances were observed in which the death of the parent female had resulted from the perforation of the wall of the uterus by the larvae. In most of the cases of uterine incubation in the family, however, it is only partial and is completed while the egg is carried on the ovipositor or after deposition upon the host. In the above two species of *Paniscus* and in *Polyblastus strobilator*, the anterior portion of the body of the larva is usually found to be extruded from the egg at the time of deposition upon the host. Vance (1927) observed

that the eggs of *Paniscus spinipes* Cush. and *P. sayi* Cush. are in various stages of development when laid, and some of them require a period of external incubation of 6 to 8 days. This variation is apparently correlated with the availability of hosts, and when these are abundant and other conditions are satisfactory the eggs are deposited rapidly and before appreciable embryonic development has taken place.

Clausen's (1932*a*) observations on a series of species of the genera *Tryphon*, *Exenterus*, *Anisoctenion*, and *Polyrhysia* revealed that no uterine incubation takes place in these forms. The first-instar larva of *T. incestus* is not fully formed in the egg until six to eight days after it is laid, and embryonic development of the eggs of *T. semirufus* Uch. does not progress appreciably so long as the host is active and feeding. In both species, actual hatching takes place only after the host has formed its cocoon. The factor responsible for hatching is evidently atmospheric humidity, which has a softening effect upon the tough eggshell. Precocious hatching was readily induced by confining active host larvae bearing eggs in closed containers with foliage, this resulting in high humidity and in moisture condensation on the surface. Morris *et al.* (1937), in discussing the habits of *E. tricolor* Roman, point out the necessity for delay in hatching until the host cocoon is formed, for otherwise the larvae will inevitably be lost either during the molts intervening between hatching and the cocooning of the host or during the spinning of the cocoon. In the Paniscini at least, the larvae of which remain firmly anchored in the eggshell, there is, because of this habit, no need for delayed hatching. Morris (1937) found that the eggs of *E. abruptorius* often do not hatch until one month or more after deposition.

Cushman's observations on *Lysiognatha* spp. indicate that hatching of the eggs in the Lysiognathinae is likewise delayed until the formation of the pupal cell of the sawfly host in the soil, and evidence points to the prolongation of the incubation period to as much as two months.

The manner in which hatching takes place is not uniform for all members of the Tryphonini. In *Paniscus*, the chorion splits longitudinally along the median ventral line and at the front, and the shell consequently becomes a shield over the dorsum and sides of the posterior segments. The eggs of *Tryphon* likewise hatch by means of a longitudinal split which extends halfway from the anterior end. In *Exenterus* and *Anisoctenion*, which embed the eggs in a wound in the host skin and leave only the dorsum exposed, a different procedure is necessary to accomplish hatching externally. The embryo is U-shaped as it lies within the egg, with the head bent back over the dorsum, and the mouth parts of the larva are consequently in contact with the dorsum of the egg, which makes external emergence possible.

The larvae of a number of groups have the habit of retaining a connection with the eggshell during the greater portion of their development. This requires, of course, that the egg itself shall be firmly attached to the body of the host. In the Paniscini, this is accomplished by a pedicel inserted through a puncture in the integument, which effectively prevents loss at molting. Appreciable larval feeding does not begin until the caterpillar host is full grown and has formed its cocoon or pupation cell. The spined tip of the abdomen of the parasite larva is held in the eggshell, and the successive exuviae envelop the posterior end of the body of the older larvae. This connection is usually broken at the beginning of the last larval stage. In *Phytodietus segmentator* Grav., parasitic upon *Loxostege* in Russia, the connection is maintained even through the last stage (Anisimova, 1931).

In the Lysiognathinae, the habits of the young larvae have been observed by Cushman in several species of *Lysiognatha*, and the pedicellate eggs of this group serve to anchor the larva in the way stated above.

The eggs of the Polysphinctini are attached not by a pedicel but instead by a large quantity of mucilaginous material. The danger of loss by molting of the spider host is obviated by the effect of the sting at the time of oviposition, which usually inhibits transformation to the next stage.

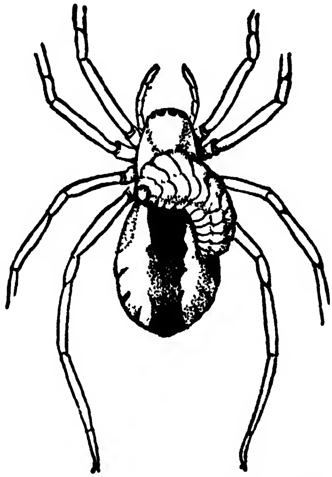


Fig. 31.—A larva of *Polysphincta dictynae* How. in characteristic position upon the abdomen of its spider host. (*From Howard*, 1888.)

The tip of the abdomen of the parasite larva remains in the eggshell; as a further aid, the first cast skin adheres firmly to the body of the host, and the later instars are provided with paired fleshy processes on the venter of the abdomen, which are fixed in the exuviae. Each lateral pair apparently serves in pincer-like fashion to hold a fold of the exuviae. There are thus two points of attachment of the larva rather than only one, and this serves a good purpose, inasmuch as the host is free-living and active until the parasite attains the last stage of larval development. The hosts of the Tryphonini and Lysiognathinae, on the other hand, are active at the time of oviposition by the parasites, but the latter do not grow appreciably until the cocoon or cell is formed and the host is quiescent. In consequence of this, a much less firm attachment is required; in fact it appears to be unnecessary after the first molt.

The encystment of the primary larva of a species of Ichneumonidae is recorded by Plotnikov in the case of *Heteropelma calcator*. The cyst is stated to consist of an outer membrane, lacking nuclei, within which occur large nucleated cells and a cellular protoplasm, and the cyst may originate from the fatty tissues of the host. That it is of host origin is unquestionable; for the egg is deposited in the mouth or in the posterior end of the intestine, and the newly hatched larva must consequently be an active form capable of penetrating the intestinal wall at one end or the other of the digestive tract. This precludes the possibility of the cyst, which envelops the larva after it reaches the body cavity, being a persistent trophamnion. The winter is passed as a first-instar larva within the cyst, which breaks down at the beginning of activity in the spring.

Tothill (1922) discusses what is termed the "feeding embryo" in *Therion morio* F., an internal parasite of the larva of *Hyphantria*. Immediately after hatching of the egg, the larva is found to be enveloped in an embryonic membrane. This membrane, or sac, persists until the second larval stage, and through it the larva derives its liquid food. It is concluded that the essential function of this sac is for protection of the parasite from the phagocytes of the host during the changes incident to its pupation.

In *Collyria calcitrator*, the first-instar larva apparently encysts itself for transformation to the following instar (Salt, 1931*b*). This usually takes place in prominent evaginations of the skin of the host, always in the lateroventral region of the body, which may be the result of hypertrophy of the hypopleural areas. The origin of the cyst is uncertain, "but it is probably part of the cast cuticle of the first stage." If this is the true explanation, there is no real encystment such as is found in other species.

Wardle (1914) has observed what are apparently mature first-instar larvae of *Hypamblys albopictus* still contained within the egg and suggests that no direct feeding takes place in this stage.

Rosenberg found young larvae of *Trichomma enecator* Rossi, presumably of the second instar, in hibernating codling-moth larvae; each one was enveloped in a translucent cyst, or trophamnion. The envelope was closely attached to portions of the fat body of the host and to the tracheae. This attachment is apparently brought about by mere contact; as the cyst enlarges with the growth of the larva it comes in contact with additional tracheae and other portions of the fat body, and a continually increasing attachment is thus established.

The persistence of the trophamnion as a partial or complete envelope about the first-instar larva after hatching is not of so frequent occurrence in this family as in the Braconidae. This infrequent occurrence is cor-

related with a reduction in the functioning of the membrane in the egg, as reflected in a relatively slight enlargement of the embryo during the incubation period.

In the case of superparasitization of the host by an internal parasite that is solitary in habit, the surplus individuals are usually eliminated in the first stage, and frequently immediately after hatching. In a number of species, it has been established that this is the result of combat between the larvae, in which the oldest and strongest is presumably the victor. When several instars are present in the one host, the youngest is usually victorious because of its better fighting equipment and greater mobility. In *Eulimneria crassifemur* Thoms. (Thompson and Parker, 1930), a few larvae are killed by combat but the majority are believed to die through the effect of a cytolitic enzyme given off into the blood stream of the host by the larva that hatches first. Some of the younger individuals die before complete issuance from the egg is accomplished. The mandibulate second-instar larva of *Collyria calcitrator* is much better equipped for combat than are other instars, and consequently this, rather than the first instar, is responsible for the death of the surplus individuals (Salt, 1931).

Among the solitary external parasites, the excess individuals are most frequently destroyed by the first larva that hatches, and this is accomplished not only by combat between those of the same stage of development but frequently by attack upon the remaining unhatched eggs.

Among the species that develop externally upon a host contained in a cell of some sort, it is the general habit of the first-instar larva to move about freely over the body and to change the point of feeding frequently. Extreme activity by the first-instar larvae is particularly evident in the Cryptinae, and it has been observed that they frequently leave the host cocoon and wander away if an aperture can be found. This activity is greatly reduced after the first molt, and only a single feeding puncture may be made thereafter. In the various groups in which the larva maintains a fixed connection with the eggshell and consequently is restricted to a circumscribed area on the host body, the point of feeding is changed at least once with each molt. This is made necessary by growth of the larva, because of which the head becomes increasingly distant from the point of attachment of the posterior end of the body.

The most extensive feeding by external parasite larvae usually takes place in the last larval stage, in which suctorial action is replaced by direct feeding upon the body tissues. In *Megarhyssa curvipes* Grav., however, it is stated that no feeding takes place in this stage. The endoparasitic forms that pupate outside the host body complete their larval feeding before emergence, though it is stated that the larva of *Thersilochus conotracheli* emerges from the host larva and continues its

feeding externally, during which time it completely drains the fluid contents from the body. This habit is much less common, however, than in the Braconidae.

Occasionally a species that is normally an external parasite of larvae hosts will develop as an internal parasite of the pupa of the same species. Husain and Mathur (1924) state that *Melcha nursei* Cam. attacks either the mature larva or the pupa of *Earias* in the cocoon and deposits its eggs externally and that larval development then takes place either externally or internally. This course of events appears improbable and requires verification.

The occurrence of a distinct larval diapause has been established in *Exeristes roborator* F. by Baker and Jones (1934). Various factors doubtless influence the tendency to enter this condition, though heredity apparently is not involved. Almost any change in external conditions adverse to normal development causes some larvae to pass into diapause. Thus a considerable percentage of larvae are in diapause during the winter months. This has no relation to the number of generations intervening since the last diapause. Even when subjected to favorable temperature and humidity conditions, the larvae will persist in that condition for several months. Higher temperatures merely increase the mortality, but the diapause may be broken by exposing the larvae to low temperatures (0.5 to 1.7°C.) for about 70 days, followed by a further period under normal developmental conditions. In the second brood of *Spilocryptus extrematis*, about half the larvae progress immediately to the adult stage, and the remainder go into diapause and become adults the following summer. Occasional individuals persist in the larval stage until the second season following.

In the instances just cited, the species are in the mature larval stage when they go into diapause, and this is undoubtedly of much the most frequent occurrence. It is interesting to note, however, that even the first-instar larvae may undergo a protracted period of quiescence; the observations of Morris on *Exenterus abruptorius* in Central Europe are of particular interest. He found that about 15 per cent of the larvae of this species proceed immediately with their development to maturity feeding being completed in two or three weeks, while the remainder persist as first-instar larvae in the sawfly cocoons for about two months. This quiescent period occurs during midsummer, but activity begins in sufficient time for the completion of larval development by the end of September. The factors responsible for this diapause are not clearly understood, for they appear to have no relation to climatic conditions.

A great many of the endoparasitic species pass a variable and often protracted period as first-instar larvae within the host body. This, however, is not a diapause, inasmuch as it represents merely a cessation

of development for a period which is determined by the cycle of the host. In this and other families and orders, the parasitic species often delay larval development until a certain stage of the host, most frequently the prepupal, is attained, at which time the body contents are presumably most suitable for the nutritional requirements of the parasite.

The larvae of species of Ichneumoninae that develop in the cells of bees have a specialized feeding habit; they are first predaceous upon the early stages of the host and then complete their development upon the food that was provided for the latter. The young larva of *Grotea anguina* sucks out the contents of the egg of *Ceratina dupla* or destroys the newly hatched larva before beginning its feast on the beebread. In the case of *Macrogrotea gayi* Brethes and *Echtropsis porteri* Brethes, some feeding may take place on the stored food immediately after hatching, but the host egg or larva is very soon destroyed (Janvier, 1933). Both these species may likewise devour the occupants and food contents of several cells before reaching maturity.

Larval hosts that are attacked by internal parasites and that continue feeding during a considerable portion of the developmental period of the latter react in several ways to the presence of the parasite within the body. Often such individuals will be of smaller size than healthy larvae of the same age, and, toward the end of the period, they show an appreciable difference in color. Another effect of parasitism is in prolonging the active larval period of the host. The healthy larvae of the larch casebearer, *Coleophora laricella* Hbn., usually spin their cocoons in May whereas those which are parasitized by *Angitia nana* Grav. persist in the active stage beyond this time before death occurs. Candura (1928) found that larvae of the Mediterranean flour moth parasitized by *Nemeritis canescens* Grav. acquire a solitary habit and produce an abnormal amount of silk in the formation of the web.

The pupation habits of the various members of the family show very little uniformity. Species that reach larval maturity in or on host larvae in a cocoon, soil cell, tunnel, or other protected place may spin a cocoon or may pupate without it. *Megarhyssa* and *Xylonomus*, which parasitize wood-boring larvae and are consequently well protected, spin tough cocoons in the tunnels, whereas *Collyria calcitrator* and *Scambus detrita* Holmg., which attack *Cephus* larvae in grain stems, do not form cocoons. When larval maturity is attained internally in lepidopterous pupae, the parasites pupate *in situ*, with the body lying in the thoracic region, oriented in the same way as the host, and a light cocoon may be spun. Usually the greater portion of the abdominal region, which contains a large quantity of waste material, is partitioned off by a plug of silk. In dipterous puparia, no cocoon is spun, and the pupa lies with its head at the anterior end. According to Voukassovitch, the ichneumonid

larvae which kill the mature host larva in its cocoon consistently orient themselves for pupation so that the head lies at the end opposite the host remains.

Some species, such as *Ephialtes examinator* F., may reach larval maturity in either the larva or pupa of the host. If in the former, the parasite larva leaves the body before pupation, whereas in the pupa it transforms *in situ*, as previously described.

A number of species of Ichneumoninae that are gregarious in habit and reach larval maturity after the host has spun its cocoon spin their own cocoons longitudinally within that of the host. These may be so numerous as to pack the interior of the cocoon and, in cross section, they are closely pressed together and give a distinctly honeycombed appearance.

In those species of the family which are internal parasites of free-living larvae and complete their development before the host spins its cocoon or forms a pupation cell, the cocoon is often spun within the host skin, with the head of the pupa directed toward the anterior end. The mature larva of *Anilastus ebeninus* Grav. (Faure, 1926) makes an incision in the venter of the body of the *Ascia* larva, secretes a quantity of mucilaginous material which binds it to the leaf, and then spins the cocoon within the empty skin. *Hyposoter pilosulus* Prov. lines the skin of *Hyphantria* with silk and pupates within it, and *Ophion chilensis* Spin. and *Nemeritis canescens* have a similar habit. The larvae of *Hyposoter disparis* Vier. and *Amorphota orgyiae* How., on the other hand, emerge from the host larvae and form their cocoons on the foliage near by.

There is a considerable diversity in form in the cocoons of the Ichneumonidae, and some bear distinctive color markings. Those of *Polysphincta* are usually found suspended in the webs of the host spiders, and they may range from an exceedingly light network of silk, through which the pupa can be clearly seen, to a very compact-walled, fusiform cocoon. Some of the latter bear pronounced longitudinal ribs, and in *P. pallipes* Holmg. the cocoon is square in cross section. According to Lichtenstein and Rabaud (1922), some species of the genus, as *P. percontatoria* Mull., leave an opening at the posterior end of the cocoon, through which the prepupa ejects the string of meconial pellets. The cocoons of this genus are normally suspended in a vertical position in the host web, with the anterior end of the pupa downward.

Several multibrooded species exhibit an unusual adaptation to external conditions in the production of winter cocoons that are of quite different form and color from those produced in the summer generation. This was first pointed out by Howard (1897) in the case of *Scambus coelebs*. In *Eulimneria crassifemur*, the summer cocoons are thin and whitish and have a distinctly paler ring about the middle, whereas the

winter cocoons are oblong-oval in form, of solid texture, and range in color from light gray to almost black (Thompson and Parker, 1930). Some of the lighter colored specimens of the latter form exhibit a faint whitish ring about the middle, but this is entirely lacking in the darker cocoons. The summer cocoons have been found only in northern Italy, the southern limit of distribution of the species, and in that section both forms are produced by the summer generation and the adults emerge from both before winter. The occurrence of two types of cocoon has also been pointed out in the case of *Aenoplex carpocapsae.*

The most striking illustration yet observed of dimorphism among the cocoons of the Ichneumonidae is found in *Sphecophaga burra* Cress., a parasite in the nests of *Vespa.* This was first noted by Cushman and later discussed at some length by Schmieder (1939). The cocoons designated as typical are thick-walled, tough, and brown in color and are firmly attached to the bottom wall of the host cell, whereas the second form is of a delicate and fluffy texture and is loosely attached to the cell wall at any point. The brown cocoons were twice as numerous as the white ones; and in many instances the colony, consisting of one to four, comprised only this form. A smaller number of cells, representing one-fourth of the total of those examined, contained cocoons of both forms, indicating that they are from the same parent and from eggs deposited at the same time. Larvae contained in typical cocoons invariably go into diapause, and the adults do not emerge until the following spring, whereas those in the white cocoons progress to the adult stage and emerge without delay.

"Jumping cocoons" are known to occur in several species of *Bathyplectes* and *Eulimneria.* Those of *B. corvina* Thoms. exhibit this peculiarity, whereas it does not occur in *B. curculionis,* a parasite of the same host and of similar habits otherwise. The cocoon of *B. corvina* has been observed to "jump" as much as 1 in. from a solid substratum, and this action is apparently accomplished by a sudden straightening of the body of the larva within it, resulting in the ends of the body striking the cocoon wall with considerable force. This peculiar adaptation, the significance of which is obscure, brings to mind the well-known jumping bean of Central America, which contains the larva of a caterpillar, *Carpocapsa saltitans* Westw.

The Life Cycle.—Many species have only a single generation each year, the cycle usually being correlated with that of the host, and the greater part of the year is passed as an inactive larva. *Diplazon laetatorius,* on the contrary, has up to 10 generations each year, and *Nemeritis canescens* 8. Faure found that the cycle of *Anilastus ebeninus* may be completed in a minimum of 18 days, which is a considerably shorter period than is required for its hosts *Ascia* spp. and others. This differ-

ence in the cycle of parasite and host is viewed as a defect in adaptation, though it should be a decided advantage if the broods of the host are overlapping. In other multibrooded species, the cycle of the summer generations ranges in length from a minimum of 11 to 14 days in *Tromatobia rufopectus* Cress. to nearly two months in many others. The actual feeding period of the larva of many ectoparasitic species covers only 3 to 6 days, though in the Tryphoninae, particularly *Paniscus*, it may be considerably longer and covers 14 to 17 days in *P. cephalotes* Holmg. The egg stage may be a good deal prolonged in those species of the subfamily in which uterine incubation does not occur, and the actual duration is governed principally by the age of the host individual attacked. In *Pimpla instigator*, there is an unusual difference in the life cycles of the two sexes, the males requiring only 16 to 17 days as compared with 24 to 28 days for the females.

A number of multibrooded species are known to have long and short cycle phases, with a portion of each brood going into diapause for a considerable period, often until the following season, whereas the remainder complete their cycle quickly. McClure (1933), in rearing a male brood of *Aenoplex carpocapsae*, found a wide range in the time required for development from egg to adult. The majority were of the short-cycle phase, completing development in about 19 days, as compared with 71 days for the long-cycle individuals. This difference in time is taken up almost entirely in the larval resting stage. Janvier found that emergence of adults from a group of cocoons of *Cryptus horsti* formed at the same time extended over a period of several months.

The species of *Polysphincta* usually have two generations each year, and there is a great variation among individuals in the duration of the larval stage. Nielsen points out the very unusual capacity of larvae of this genus to undergo prolonged periods of inactivity. When the spider host is without food, the parasitic larva apparently refrains from feeding and still is able to live for several months. Development is resumed as soon as host feeding again takes place.

Hibernation takes place most commonly in the mature larval stage in the cocoon. This applies particularly to the Cryptinae, Tryphoninae, and Ichneumoninae, of which a considerable number of species have been studied. In the latter subfamily, *Collyria calcitrator* is an exception; it passes the winter as a third- or fourth-instar larva in the living sawfly host. *Glypta rufiscutellaris*, a parasite of the larvae of the oriental fruit moth and others, passes the winter as a mature larva in the cocoon and has three generations per year, corresponding to the cycle of the host. *G. haesitator* Grav., which attacks the closely related *Cydia nigricana* Steph., a single-brooded host, has only one generation and passes the winter as a second-instar larva within the living host. *Cremastus*

flavoorbitalis, *Heteropelma calcator*, and *Therion morio* hibernate in the first larval stage within the host, and in several species the larva is enveloped in a cyst during this entire period. Some species of *Polysphincta* appear to pass the winter in the early larval stages upon the body of the host. Nielsen states that young *Theridium lunulatum* coming out of hibernation in the early spring bear the small parasite larvae upon the body.

Phaeogenes nigridens is said to persist only as adult females; and, according to H. D. Smith, the majority of species of the family that hibernate as adults belong to the Joppinae. A number of Ophioninae have the same habit, and *Hyposoter disparis* and *Thersilochus conotracheli* attain the adult form during the autumn but remain within the cocoon until spring. Both Seyrig (1924) and Townes (1938) mention the finding of adult females of many species of Ichneumoninae during the winter, some species being consistently under bark, whereas others are in empty tunnels in decaying wood, in clumps of dry grass, or in other sheltered places.

Sex Ratio and Parthenogenesis.—The sex ratio of the species that normally reproduce bisexually has been determined in only a relatively few instances. Usually there is a slight preponderance of females, with the greatest excess recorded in *Pimpla pomorum* Ratz., which has a sex ratio of 4 to 1. In a few species, however, the males are said to predominate under field conditions. It has been shown by Chewyreuv (1913) and later authors that the sex of the parasite progeny is correlated with the size of the hosts in which development takes place. The males develop very largely in small hosts and females in the larger ones. This is most evident among species attacking pupae and explains the differing sex ratios secured for a species on several hosts and at different seasons.

In his work with *Pimpla* spp., Chewyreuv found that large host pupae from the field consistently yielded a high percentage of females, whereas the smaller hosts produced mainly males. Laboratory tests supported these findings; for all large pupae produced females, and 80 per cent of the small ones yielded males. This disparity in sex ratio is attributed to selective oviposition by the parasite female. When oviposition takes place on or in the host larva at almost any stage of its development, and the host is killed only after the cocoon is formed, as in those attacked by *Exenterus* and *Campoplex*, the mechanics of this selective process are more difficult to determine than when attack is upon the pupa, which is already at its full size.

Several species are known to reproduce unisexually, the females giving rise to progeny of the same sex without the intervention of the male. Orlova records the production of 26 consecutive generations of *Hemiteles areator* Panz. without the appearance of a single male, though Muesebeck and Dohanian (1927) found that the unmated females

produced only males. They record the production of 12 generations of females of *H. tenellus* Say in three years and state that the male is unknown. *Nemeritis canescens*, *Sphecophaga burra*, and *Polysphincta pallipes* reproduce in the same way, and the large-scale rearings of the first-named species by various workers have revealed only an occasional male.

Reproductive Capacity.—The reproductive capacity of the Ichneumonidae is exceedingly variable. *Phaeogenes nigridens* is said to deposit a total of only approximately 50 eggs, and many Ichneumoninae probably do not greatly exceed this number. *Exeristes roborator*, however, was found by Baker and Jones to deposit up to 40 eggs per day and a maximum of 679. In the Ophioninae, the number is often considerably higher. The maximum recorded is for *Hyposoter disparis*, of which a series of females produced an average of 561 eggs and one individual deposited 1,228 (Muesebeck and Parker, 1933). An examination of the ovaries of a number of species revealed the presence of a total of 200 to 400 eggs in various stages of development. Meyer (1926) states that *Angitia fenestralis* Holmg. is able to produce a total of at least 540 eggs. Among the Tryphoninae, the capacity is usually relatively low, though females of *Hypamblys albopictus* are stated to contain up to 448 eggs. In this subfamily, there is a marked disparity in the reproductive capacities of the ectoparasitic and the endoparasitic species.

In general, there are two to eight mature eggs in each ovariole, which presumably represents the potential daily capacity. Thus the number of ovarioles governs the rate of egg deposition. *Glypta rufiscutellaris* and *H. albopictus* have the largest number recorded, which is approximately 56, whereas the majority of the Ichneumoninae, Cryptinae, and the ectoparasitic Triphoninae have a smaller number, ranging from 8 to 16.

IMMATURE STAGES

The Egg.—The eggs of the great majority of species of the family are of simple form, without a stalk or pedicel and usually with no sculpturing of the chorion. The shape is variable, ranging from the broadly oval to cylindrical and, in this simple form, to the extremely slender form represented by those of *Echthropsis porteri* and *Perithous mediator* Grav., which are only one-twentieth as wide as long, curved, and with both ends tapering to points. The eggs of the Cryptinae, Joppinae, Ichneumoninae, and Ophioninae are, with few exceptions, of the above general form. In the latter two subfamilies, the stalked type of egg is also found, the extreme development of this modification being in the genera *Rhyssa* and *Megarhyssa*, in which the anterior end is drawn out into a slender tube. The stalk of the egg of *R. persuasoria* is approximately four times the length of the egg body, and the total length of the egg is 12.0 to 13.5 mm.

Surface sculpturing on the chorion occurs in only a few species of the above subfamilies and is not elaborate. In *Cryptus sexannulatus* Grav. the egg bears light longitudinal markings, whereas that of *Ephialtes extensor* (Fig. 32*E*) is covered with closely

set "bosses" arranged in rows. The color is usually translucent white, with the eggs of a few species assuming a brownish tinge as incubation progresses.

The eggs of the Ophioninae are usually of the normal kidney-shaped or elongate form, but several genera reveal an adaptation for attaching them to the integument of the host larva. This modification is represented by a "pad" or "button" at the mid-ventral side of the egg by means of which it "adheres" to the inner side of the integument of the host at a point in the body opposite that at which the ovipositor is inserted. This form is represented by *Therion morio* (Fig. 32*C*), and one that is apparently similarly modified is described by Plotnikov (1914) in *Heteropelma calcator*.

The most striking modifications in egg form occur in the ectoparasitic species of the Tryphoninae and Lysiognathinae; in these groups, the eggs either are partly embedded in a puncture in the integument of the host larva or have an adaptive modification of the chorion at the *posterior* end into some form of anchor, which is

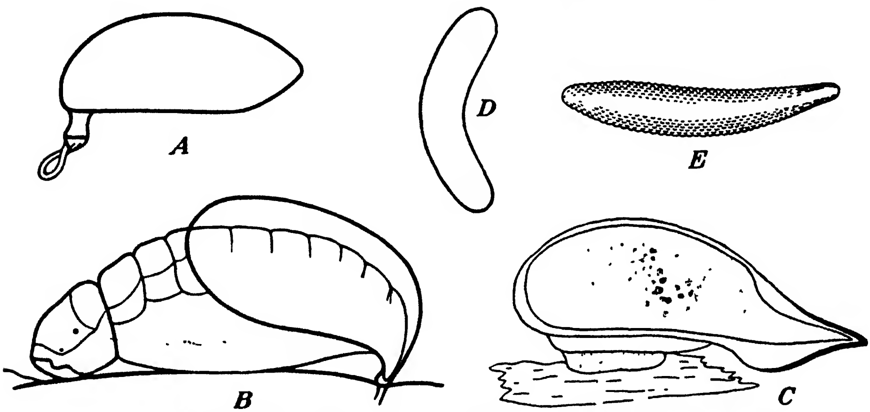


FIG. 32.—Immature stages of the Ichneumonidae. *A*, egg of *Paniscus testaceus* Grav.; *B*, first-instar larva of *P. virgatus* Four. with posterior half of body encased in the egg shell; *C*, egg of *Therion morio* F. after eight days' incubation; *D*, egg of *Pristomerus vulnerator* Panz.; *E*, egg of *Ephialtes extensor* Tasch. (*A from Martelli*, 1909; *B from Newport*, 1852; *C from Tothill*, 1922; *D and E from Rosenberg*, 1934.)

embedded therein. In the Paniscini, this adaptation (Fig. 32*A*) uniformly appears as a short, blunt pedicel, situated somewhat ventrally, from which extends a spiral, looped or "braided" process that is stated to be very elastic at the time of deposition. Only this latter portion is embedded in the wound. Chewyreuv points out that the pedicel is not an extension of the egg chorion, for it dissolves completely in potassium hydroxide. Associated with this form of egg is a distinctive coloration, the chorion being black or brown and shining, thus making it conspicuous upon the body of the host. The darkening of the chorion is most pronounced in the Paniscini and is of varying extent, and at times entirely lacking, in the Tryphonini.

The extreme modifications in egg form are found among the Tryphonini and Cteniscini. Several of these have been described and figured by Clausen (1932*a*). The egg of *Tryphon semirufus* (Fig. 33*H*) has a long thread-like pedicel, twice the length of the egg body, which bears at its distal end a long, heavily pigmented bar, attached at the middle and serving as an anchor deep within the tissues of the host. Bischoff (1923) figures an identical egg for an undetermined tryphonine species in Europe; that of *T. rutilator* Holmg., the ovarian form of which is illustrated by Pampel, is evidently very much like it. The egg of *T. incestus* (Fig. 33*A*, *B*) is of the same general form; but the pedicel is shorter, the anchor much smaller, and

the latter is inserted immediately beneath the integument. That of *Tricamptus apiarius* Grav. figured by Bischoff is similar to it. The egg of *Exenterus tricolor* Roman (Morris *et al.*, 1937) is of the same general form and bears a scale-like sculpturing. In these species, the chorion is exceedingly heavy and tough and is difficult to puncture, even with a needle. In *Anisoctenion alacer* Grav. (Fig. 33*D*, *F*), the anchor assumes a curious and quite different form, in which it is represented by a blackened shield, with serrate margins, on the ventral side of the egg body. This shield, which is slightly larger than the egg, opens out, umbrella-like, at the time of

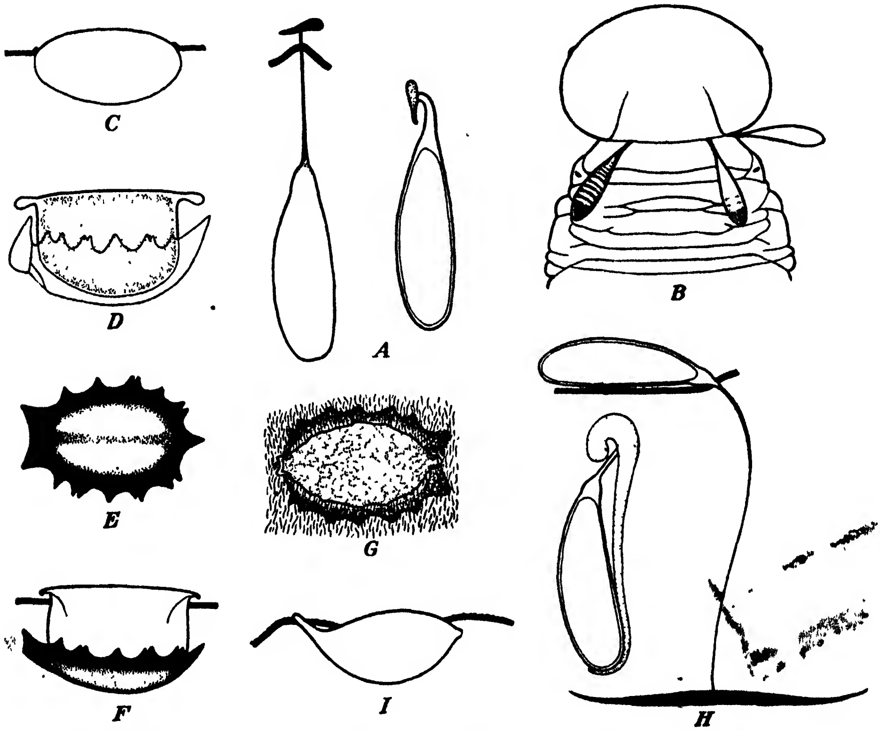


FIG. 33.—Eggs of the tryphonine Ichneumonidae. *A*, ovarian and laid egg of *Tryphon incestus* Holmg.; *B*, the same *in situ* upon the neck of a *Lophyrus* larva; *C*, egg of *Exenterus coreensis* Uchida embedded in the skin of the host larva; *D*, ovarian egg of *Anisoctenion alacer* Grav.; *E* and *F*, laid egg of same, ventral and lateral views; *G*, dorsal view of same, with the shield visible through the host skin; *H*, ovarian and laid egg of *Tryphon semirufus* Uchida; *I*, laid egg of *Exenterus abruptorius* Thbg. (*A–H from Clausen*, 1932; *I from Morris*, 1937.)

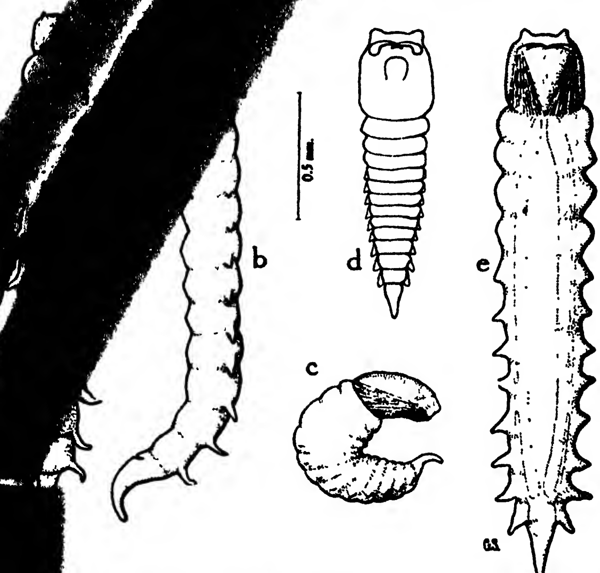
deposition. The entire egg except the dorsal surface lies beneath the host integument, and the exposed portion of the chorion bears delicate reticulate markings.

The egg of *Lysiognatha* sp. (Cushman, 1937) is apparently quite similar to that of *Tryphon incestus*. In all the species that deposit eggs of the pedicellate type, the adaptations that will appear in the laid egg can be detected by an examination of the ovarian egg (Fig. 33*D*, *H*).

Not all the Tryphoninae possess eggs of the pedicellate type discussed above. In the Diplazonini, the egg is ellipsoidal in form, with both ends smoothly rounded. That of *Hypamblys albopictus* is kidney-shaped, whereas the egg of *Exenterus coreensis*

Uchida (Fig. 33C) is oval in outline [illegible] ver, and is largely embedded in the wound. The egg of [illegible]) described and figured by Morris (1937) may be considered [illegible] between that of *E. coreensis* and of *Tryphon incestus*, and [illegible] pedicel formation. This is represented by a slender cylin[illegible] posterior end. At oviposition, the body of the egg is largel[illegible] nd, only a portion of the dorsum being exposed through the [illegible] nd the tip of the pedicel also protrudes, though from a se[illegible] le. The variation in egg form and manner of deposition wi[illegible] ted by the three species of *Exenterus* that have been mentio[illegible]

First-instar Larva [illegible] ned the normal hymenopteriform first-instar larva of the f[illegible] ctophagous species of the Ichneumoninae



[illegible] ure stages of *Collyria calcitrator* Grav. *a* and *b*, first-instar larva, [illegible] ws; *c*, *d*, and *e*, the second-instar larva, the last after extensive feeding.

[illegible] es; it is characterized by a large and often heavily sclerotized head, [illegible] ntennae and simple mandibles, and 13 body segments of diminish[illegible] tegument may be bare or clothed with numerous minute spines. [illegible] develop internally are of this same general form. The first-instar [illegible] bears six pairs of small setae on each segment; in addition, each [illegible] bears a broad transverse band of minute integumentary setae. [illegible] usually situated dorsally, though it is said to be on the venter [illegible] egment in *C. calcitrator* (Fig. 34*a*). In this species, paired fleshy [illegible] solaterally on the abdomen; they are of increasing length on the [illegible].

[illegible] i, the first-instar larva has been described only for *Paniscus* [illegible] It differs from the normal hymenopteriform larva only in the [illegible] rous forward-directed spines on the venter and sides of the last [illegible], an adaptation to hold the caudal end of the body more firmly

within the eggshell during [illegible]hincta, which has the same habit, is not known to possess this c[illegible]

The first-instar larva of A[illegible]. 35B) is markedly different from those thus far discussed, tho[illegible]nopteriform type. Each body segment bears a transverse ro[illegible]h lateral margin; these are of decreasing length and number o[illegible]ents. Each of the first five abdominal segments bears a prono[illegible]ian dorsal line. This larva normally moves upon its back in a [illegible]elts and the caudal sucker aiding in accomplishing locomotion, w[illegible] long hairs hold the body in a horizontal position. *Exenterus co*[illegible] several others of that genus and *Tryphon semirufus* have sim[illegible] lateral tufts of hairs on the latter are much shorter. The lar[illegible] (Fig. 35C), however, lacks both the dorsal welts and the lateral [illegible]ensely clothed with minute spines, and does not assume an inver[illegible]novement.

A *B*

Fig. 35.—First-instar larvae of the tryphonine Ichneumonidae. *A*, [illegible] Uchida; *B*, *Anisoctenion alacer* Grav.; *C*, *Tryphon incestus* Holm[illegible] 1932.)

The most common type of first-instar larva among the end[illegible] the caudate, which attains its highest development in this family. [illegible] or less cylindrical, with 11 to 13 recognizable segments, and the in[illegible] smooth and shining. The tail may equal or exceed the body len[illegible] slender and taper to a sharp point or be almost cylindrical, with th[illegible] rounded, as in *Thersilochus conotracheli* (Fig. 36*B*, *C*). In some sp[illegible] *cerinops* Grav., the terminal portion of the tail is spined. Timb[illegible] sidered the tail of *Eulimneria valida* Cress. to be a blood gill, wh[illegible] ramifications of the tracheal branches in the tail, illustrated by[illegible] the larva of *Hyposoter pilosulus*, which led him to attribute a r[illegible] to that organ, have been shown by Thompson and Parker to rep[illegible] interpretation of the structures observed in mounted specime[illegible] *Eulimneria crassifemur* Thoms., a species of very similar form, th[illegible] the supposed bundle of tracheids is simply a lobe of the fat body [illegible] globules have been dissolved by the reagents employed.

Thorpe (1932) has studied the tail appendage of a series of [illegible] other families with particular reference to its role in respirati[illegible] appreciable variation in the extent to which the tracheal branch[illegible] organ. In the majority of species, the lateral tracheal trunks [illegible]

terminate in the fat body, but in *Cremastus interruptor* they branch and extend through the basal two-thirds of the tail.

The newly hatched caudate larvae of *Cremastus flavoorbitalis* Cam. (Bradley and Burgess, 1934) (Fig. 36*A*) and *C. interruptor* Grav. bear a double row of scallops transversely on each body segment; these disappear before the first molt and are believed to be an adaptation to permit of rapid increase in body size. The larva of *Anomalon cerinops* has a pair of small slender processes ventrally on the first and third thoracic and the sixth and eighth abdominal segments.

The first-instar larva of *Omorgus mutabilis* Holmg. bears a pair of prominent tusk-like sense organs on the head that project downward and backward from the posterior ventral margin of the head capsule. They represent one of the four pairs of sense organs present on the venter of the head of larvae of this family.

Many of the caudate larvae have the head comparatively large, heavily sclerotized, with falcate mandibles, approaching that of the mandibulate type. The larva of *Syrphoctonus maculifrons* Cress. may properly be considered as of the latter type, for the head is equal to the thoracic region in width and the tail is hardly evident (Kamal, 1939). It bears a strong resemblance to the mandibulate larvae of the Braconidae, particularly of *Opius*. In *Diplazon* and *Homotropus*, of the same subfamily, the head is smaller and the tail more fully developed, though still short.

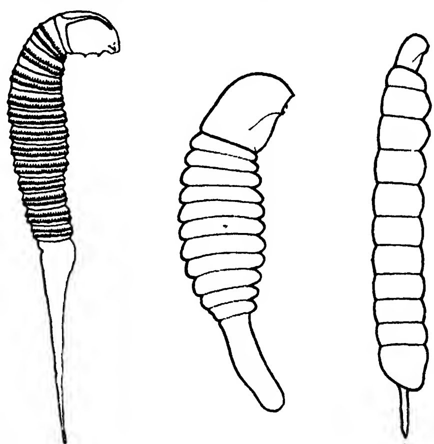


FIG. 36.—*A*, the newly hatched first-instar larva of *Cremastus flavoorbitalis* Cam. (*from Bradley and Burgess*, 1934); *B*, and *C*, first-instar larva of *Thersilochus conotracheli* Riley, before and after feeding (*from Cushman*, 1916).

The vesiculate type of larva is not nearly so common, nor is the vesicle so highly developed as in the Braconidae. Usually it is in an incipient stage, is small in size, and often is not readily recognized because of being retracted at the time of examination. A number of the caudate larvae of the Ichneumoninae and Ophioninae, such as *Glypta rufiscutellaris*, *Nemeritis canescens*, and *Anomalon cerinops*, bear the vesicle dorsally at the base of the tail. A typical ichneumonid vesicle is that of *Banchus femoralis* Thoms., illustrated in Fig. 37.

The polypodeiform type of larva is found in *Hypamblys albopictus* (Wardle, 1914) in which the paired thoracic processes are lobe-like and those of the abdominal segments rather sharply pointed. The tail is approximately one-fifth the length of the body.

There is apparently no essential distinction between the respiratory systems of ecto- and endoparasitic first-instar larvae. Some are stated to be entirely devoid of tracheae, whereas others have a complete internal system corresponding to that of the mature larva except for the lack of spiracles. The tracheal system of *Phaeogenes nigridens*, which has been fully described by Smith, consists of a main lateral trunk on each side of the body connected by main transverse commissures dorsally in the first thoracic and ventrally in the ninth abdominal segment. Accessory lateral commissures, connected with the main trunks by three branches, extend from the

posterior margin of the first thoracic to the anterior margin of the first abdominal segment. In each of the first nine abdominal segments, the ventral branches are connected to form secondary transverse commissures.

With very few exceptions, the first-instar larvae of this family lack spiracles. *Paniscus cristatus* is said to have a pair on the prothorax; Meyer (1922) illustrates that pair, and eight additional pairs on the abdomen, in *Tryphon signator* Grav. Imms (1918*b*) found nine pairs of spiracles on the first-instar larva of *Pimpla pomorum;* Speyer (1926), studying the same species, noted an additional pair, very minute, on the thorax. The general lack of an open tracheal system is in contrast to the Braconidae and other extensively studied families of the order, in which the ectoparasitic first-instar larvae are quite consistently provided with open spiracles.

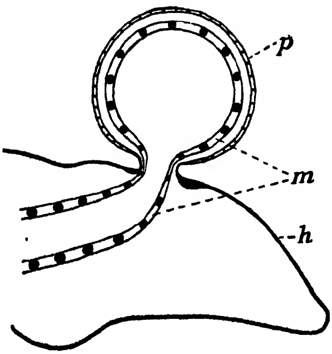


FIG. 37.—The anal vesicle of *Banchus femoralis* Thoms., showing (*h*) hypodermis, (*m*) mesenteron, and (*p*) proctodeum. (*Redrawn, after Bledowski and Krainska,* 1926.)

Intermediate-instar Larvae.—The information available is insufficient to make an adequate comparison of the larval instars between the first and last, due primarily to uncertainty as to the total number. A considerable number of species are stated to have only three instars, and others four; many are known to have five instars. Unquestionably, some of those said to have only three will reveal, on closer examination, a greater number. Rosenberg mentions the occurrence of six instars in occasional larvae of *Cryptus sexannulatus* Grav. and *Hemiteles hemipterus,* though the normal number is five and four, respectively. In the species of Paniscini and Polysphinctini that retain connection with the eggshell during larval development, the number of instars can be readily determined by a count of the exuviae forming the pad beneath the posterior portion of the body.

In species having hymenopteriform first-instar larvae, there is little change in general form in the following instars, but those of caudate form in the first instar usually show a progressive reduction in the appendage, with its complete absence in the last instar. In *Thersilochus conotracheli,* it disappears entirely with the first molt, and in some other species it persists only through the second instar. The bidentate mandibles appear in the second instar in *Ephialtes examinator.* The second-instar larva of *Collyria calcitrator* (Fig. 34*c, e*) is of a pronounced mandibulate type, with the head wider than the body and the mandibles large and falcate in form. The fleshy dorsolateral processes on the abdomen persist in this instar.

The stage of development at which the spiracles appear is variable. In *Ephialtes examinator* and *Phaeogenes nigridens* the nine pairs are evident in the second instar, though in the latter species, which is internal, they are nonfunctional. *Angitia fenestralis* Holmg. reveals the spiracles in the penultimate instar, but in the majority of species they appear only in the last one.

Mature Larvae.—The normal last-instar larva of the Ichneumonidae has 13 distinct body segments, the integument usually smooth and glistening, and it bears no fleshy processes or appendages. In *Phaeogenes nigridens,* there is a very characteristic dorsal hump on the third thoracic and first abdominal segments, a modification in form said by Smith to be necessary because of the manner of feeding of the larva. In the majority of species, the mandibles are simple, often with minute spines on the margin, though a few are bidentate and those of *Echthropsis porteri* are 5-dentate. In *Xylonomus brachylabris* Kr., the mandible has a concavity on the inner side flanked

by ridges crowned with distinct teeth. The mandibles of *Polysphincta* are stated to be curved outward at the tips, and the puncture in the host integument is made, not by a pinching action, but by the tips being brought together, inserted, and then spread apart. Each body segment usually bears a row of small, delicate spines transversely that may encircle the segment. In *Philopsyche abdominalis* Morley (Skaife, 1921*b*), there are two distinct bands of short spines on each segment, those of the first band being directed cephalad and those of the posterior band caudad. This is presumably an adaptation for movement within the case of the bagworm host. The larva of *Pimpla pomorum* bears numerous minute papillae upon the integument.

The tracheal system consists of the two main longitudinal trunks connected by dorsal anterior and ventral posterior commissures, with a supplementary lateral trunk on each side extending from the posterior margin of the first thoracic segment to the anterior margin of the first abdominal segment and connected with the main trunk by three branches. There are usually nine pairs of spiracles, the first of which, though mesothoracic in origin, is situated at the posterior margin of the prothorax, the remainder being near the anterior margins of the first eight abdominal segments (Fig. 38). *Angitia fenestralis* (Meyer, 1915) is stated to have 11 pairs of spiracles, situated on all thoracic and the first eight abdominal segments. Imms (1918*b*) has called attention to the occurrence of 10 pairs in *Pimpla pomorum*, the additional pair on the second thoracic segment being vestigial and non-functional. Thorpe (1930) mentions this in his discussion of *P. ruficollis* Grav. and states that the occurrence of the vestigial pair on the second thoracic segment is probably general in the family but has been largely overlooked. There are 10 pairs in *Polysphincta tuberosa*, also, but those of the thorax are on the first and third segments, whereas in *Collyria calcitrator* (Fig. 38) they occur upon the second and third. The tracheal system of the latter species differs also from the normal for the family in the lack of the lateral accessory and the posterior ventral commissures. Salt points out the general similarity of the larval characters of this species to those of the Braconidae. In *Scambus detrita* and several other species, the ventral branches in each abdominal segment unite to form accessory ventral commissures.

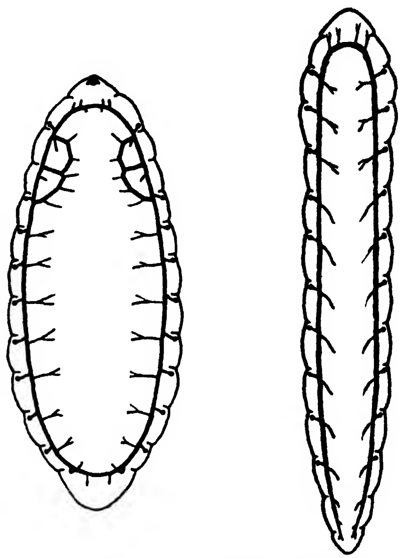


FIG. 38.—The tracheal system of mature ichneumonid larvae. The typical form (left) shows the accessory longitudinal commissures in the thorax and the arrangement of the spiracles. That of *Collyria calcitrator* Grav. at the right is an exceptional form lacking the accessory thoracic and the posterior commissures. (*From Salt*, 1931.)

The greatest modification in mature larval form and in functional adaptation occurs in the tribe Polysphinctini and in certain other Ichneumoninae. These species are parasitic upon spiders or are predaceous in their egg capsules. The morphological modifications are of two forms and serve distinct purposes. The first of these is the occurrence dorsally of retractile "welts" (Fig. 39*C*), surmounted by a number of hooked spines or of patches of straight spines, which serve to hold the larva in the web during the spinning of the cocoon or to facilitate movement in the egg capsule. The

second modification is the development of paired fleshy processes ventrally on certain abdominal segments to attach the body firmly to the exuviae and thus to the body of the host spider.

The mature larvae of a considerable number of species have been described by Nielsen (1923), and the dorsal welts, bearing the hooked spines, occur in most if not all species of *Polysphincta*, *Schizopyga*, and *Zaglyptus*. The number of welts is usually seven or eight, and they occur in a single row on the median line of the third thoracic and the following seven segments in *P. tuberosa* Grav. (Fig. 39*A*), *P. eximia* Schm., and *P. nielseni* Roman. Four welts only are recorded on the larva of *P. gracilis* Holmg., whereas in *P. clypeata* Holmg. (Fig. 39*B*), *P. pallipes*, and *S. podagrica* Grav.

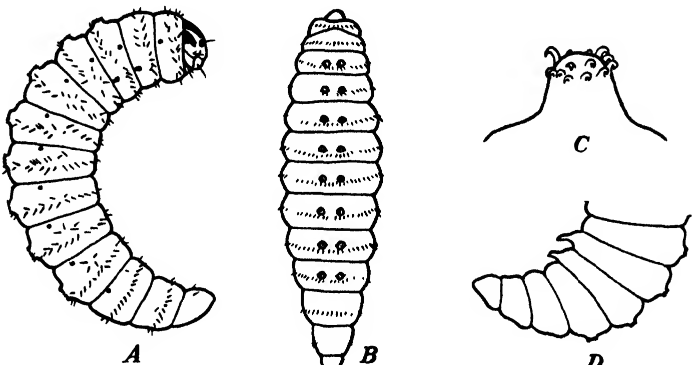


FIG. 39.—*A*, the mature larva of *Polysphincta tuberosa* Grav., lateral view; *B*, same of *P. clypeata* Holmg., dorsal view; *C*, a dorsal welt of *P. tuberosa*, much enlarged, showing the hooked spines by means of which the larva maintains its hold on a strand of the host web; *D*, the posterior segments of the larva of *P. eximia* Schm., showing the fleshy ventral processes of the fifth and sixth abdominal segments, which telescope into those of the exuviae and aid in holding the larva in position on the host. (*Redrawn, after Nielsen*, 1923.)

they are paired, rather than single, on each segment. In the last species, they occur on the first six abdominal segments (Nielsen, 1935). Laboulbene (1858) records them on the first seven body segments in *P. fairmairii* Lab., and Maneval (1936) states that they are on the first seven abdominal segments in *Z. variipes* Grav. In these two species, also, the welts are single rather than paired. The hooked spines that surmount each welt are directed outward from the center of the welt; and when one of these, or more, is drawn over a strand of the host web and the welt then retracted into the body, the larva is very securely held in position. In *Tromatobia oculatoria* F., the spines are simple and straight and arranged in transverse bands at the anterior and posterior sides of the welt. Those at the front are directed cephalad, and those at the rear caudad.

Many if not all of the species of *Polysphincta* have a pair of fleshy conical processes (Fig. 39*D*) ventrally on the fifth and sixth abdominal segments, and these are embedded in the exuviae beneath the body. They are present upon the intermediate instars, also. In *S. podagrica*, there are four pairs of these processes rather than two, and they occur on the fifth to the eighth abdominal segments.

AGRIOTYPIDAE

This family is represented by only two species, *Agriotypus armatus*, described from England by Walker in 1832, and *A. gracilis* Waterst.,

from Lake Hakone, Japan, described in 1930. Both are aquatic in habit and develop as external parasites upon the prepupae and pupae of caddis flies. *A. armatus* has since been found in various parts of Europe, and general observations upon its habits and biology, with incomplete descriptions of the early stages, have been made by Klapalek (1889, '93) and Henriksen (1918, '22). It was not until 1932 that an adequate account of its habits and descriptions of all instars were presented by Miss K. Fisher. The Japanese *A. gracilis* was observed by Ota (1917, '18), who considered it to be distinct from the European form, and its habits and early stages were later studied by Clausen (1931*b*).

BIOLOGY AND HABITS

Both species of the family pass the winter in the adult stage within the cocoon in the caddis-fly case and emerge in the spring when the water temperature rises sufficiently to induce activity, approximately to 13°C. in the case of *A. armatus*. Twenty-one parasitized caddis-fly cases containing *A. gracilis* collected at Lake Hakone, Japan, on Mar. 25 and placed in a jar of water that soon reached air temperature gave complete emergence within two hours. The females predominated in the ratio of approximately 2 to 1.

Mating takes place very soon after emergence, and oviposition follows about one week later. In order to reach the caddis-fly cases which occur upon stones, etc., at a depth of 6 to 15 in. beneath the water surface, the female crawls down a plant stem or the side of an exposed stone and searches about for them. There is apparently no attempt at swimming at any time, and consequently it is remarkable that cases parasitized by *A. gracilis* were found as much as 25 ft. distant from the nearest exposed stone or bank. When an inhabited case is found, the ovipositor is inserted for exploratory purposes. If the caddis fly is still in an active stage, this thrust causes it to extrude the head and thorax from the case, whereupon the parasite immediately leaves it and searches for another which contains a prepupa or pupa. The ovipositor is inserted, often with considerable difficulty, and the egg deposited externally. In emerging from the water, the female merely releases her foothold and floats to the surface, there being no movement of either the wings or the legs at this time. She may take wing immediately upon reaching the surface, or she may coast for several inches, with the wings beating rapidly, the middle and hind legs trailing on the water, and the forelegs sharply raised.

A. gracilis females were found to remain under water up to 14 minutes under experimental conditions, but this is probably exceeded in nature. Upon entry into the water, the body is completely enveloped in an air bubble that conforms to the body outline and encloses the antennae,

which are held back over the dorsum, and the wings. The formation of this bubble is made possible by the dense pubescence that clothes the entire body. The oxygen contained within the bubble serves to fill the requirements of the wasp while immersed, and the supply is doubtless considerably augmented from the surrounding water. The antennae, being held within the air bubble, are apparently entirely

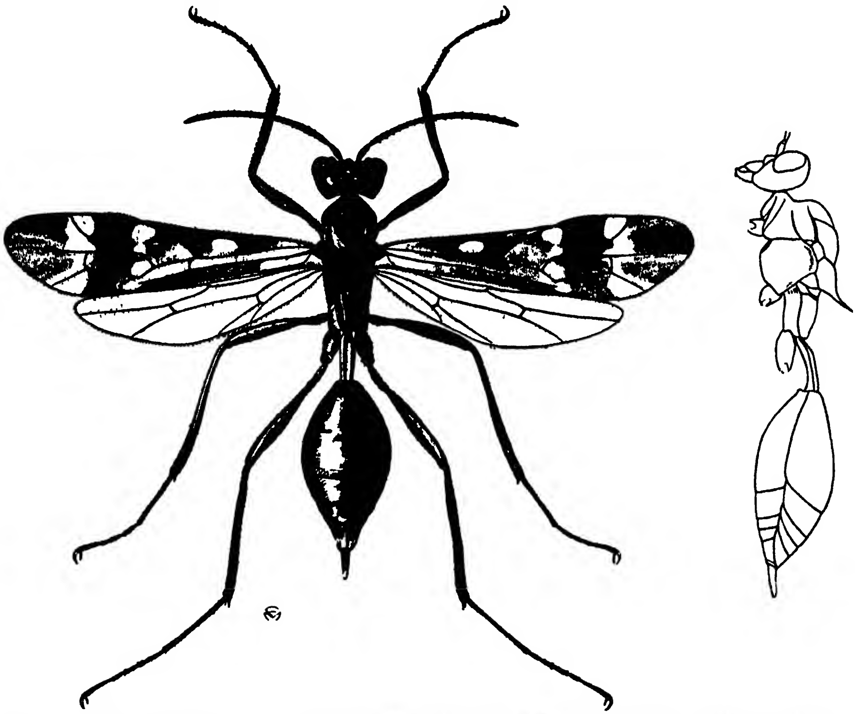


Fig. 40.—The adult female of *Agriotypus gracilis* Waterst. (*Drawing by M. F. Benson.*)

functionless in so far as locating the host and determining its suitability are concerned.

The egg is usually placed either laterally or dorsolaterally on the thorax or the anterior portion of the abdomen of the host, often in an intersegmental groove and occasionally upon a wing pad, whereas in *A. armatus* the more frequent position appears to be ventrally on the abdomen.

In the hatching of the *A. gracilis* egg, a small break is first made in the tough chorion immediately beneath the mouth of the larva, and this aperture is slowly enlarged by a steady forward thrust of the body. The head is bent back over the thorax, and the venter of the latter is forced through the aperture first. A further enlargement of the opening releases the head, and complete emergence is finally effected. The

emergence hole is circular in outline and two-thirds the width of the egg. The edges are curled back, and there is no splitting along a longitudinal line such as occurs in many other Hymenoptera. From five to eight hours are required for hatching of the larva from the egg.

The modifications in form of the first-instar larva are adaptations for locomotion and to prevent it from being washed out of the host case. The dorsal rows of spines can be raised to a nearly vertical position and serve, in conjunction with the head and the bifurcate caudal appendage, to facilitate ready movement between two curved surfaces such as are presented by the caddis-fly body and the wall of the case. Respiration is evidently cutaneous, and the oxygen supply is derived from the water that flows through the case.

The point of feeding of the young *A. armatus* larva is usually on the underside of the thorax of the prepupa and beneath a wing pad on the pupa. The first molt takes place about one week after hatching.

The occurrence of an internally parasitic phase in the development of the larva, as indicated by the supposed first-instar larva of *A. armatus* found by Henriksen (1922), is not outside the range of possibilities. Only three instars have thus far been described, all of which feed externally. The normal number of instars for the order is five, and two are consequently not accounted for. If the larva found by Henriksen proves to be *Agriotypus*, the habits and manner of development will be of particular interest. Entry into the body of the host would presumably be by the first-instar larva, followed by an immediate molt, after which two stages would be passed internally and these succeeded by the two external stages that are now known as the second and third.

After completely consuming the contents of the host body, the *Agriotypus* larva spins its cocoon within the host case. The last larval exuviae of the host, and the pupal remains, are left in pad-like form at the posterior end of the case and are partitioned off by the parasite cocoon. This cocoon lines the sides of the host case, and its wall is thickest at the anterior end. The ribbon-like appendage, so characteristic of parasitized cases, is then formed, being extruded dorsally at the anterior end of the case. This ribbon is 1.0 to 1.5 mm. in width and may be nearly 5.0 cm. in length. It consists of a closely woven outer covering enclosing a mass of tangled silken strands. Ota considers the ribbon to be a protective device, but this is improbable. That it serves a respiratory purpose is apparently certain, as the experiments of Muller (1889, '91) revealed that the larvae and pupae invariably died when the band was removed, though they survived if removed from the water. The respiratory requirements of the early larval stages upon the living host are met by the absorption of oxygen from the water flowing through the case; but after the cocoon is spun the parasite larva and its following

stages are surrounded by air, and some means are necessary to replenish the oxygen supply during the many months passed within it. The way in which oxygen from the surrounding water reaches the parasite in the cocoon has not been studied, but it is surmised that a lower air pressure within the cocoon may draw the gas from the water and through the interstices of the silken ribbon into it. Fisher concludes that the gas content of the cocoon may at first be carbon dioxide exhaled by the larva and that this escapes and is replaced by oxygen as soon as the ribbon begins to function.

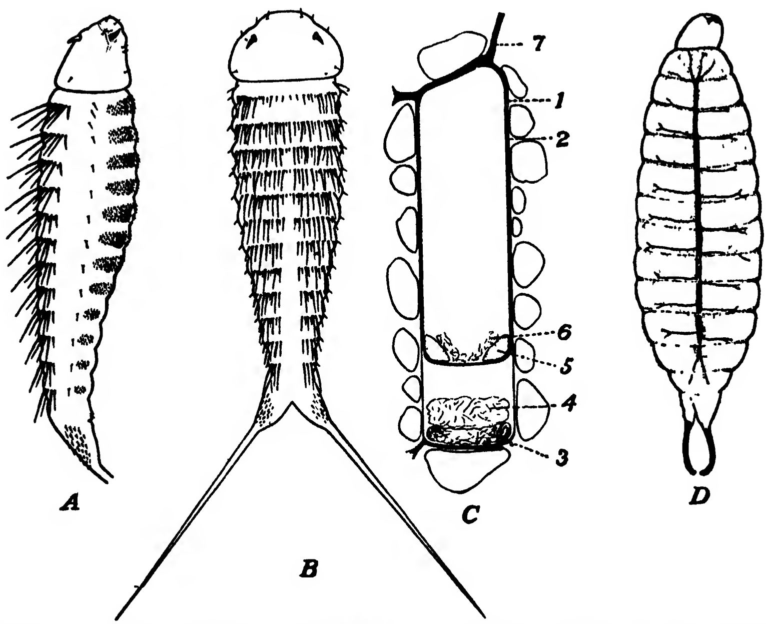


FIG. 41.—Immature stages of *Agriotypus*. *A* and *B*, first-instar larva of *A. gracilis* Waterst.; *C*, cocoon of same within caddis-fly case, showing (1) caddis-fly cocoon, (2) cocoon of *Agriotypus*, (3) larval exuviae of the host, (4) remains of host pupa, (5) and (6) larval meconium and exuviae of *Agriotypus*, (7) the silken respiratory ribbon which extends out of the cocoon into the surrounding water; *D*, second-instar larva of *A. armatus* Wlk. (*A–C from Clausen*, 1931; *D from Fisher*, 1932.)

After the cocoon is spun, the larva remains quiescent for 7 to 10 days and then transforms to the pupal stage. The meconium is cast by the prepupa and is found in the form of a ring surrounding the tip of the abdomen of the pupa but separated from it by the last larval exuviae.

There is a single generation each year; the adults usually emerge during April, and the adult stage is again attained at the end of September. At this season, the water temperature is declining, and the adults remain quiescent in the cocoon until the following spring.

IMMATURE STAGES

The egg of *A. gracilis* measures 0.9 mm. in length and 0.18 mm. in greatest width and is slightly larger than that of *A. armatus*. It is slightly convex dorsally and broadest at the anterior end, and the posterior end is smoothly rounded. The chorion is exceedingly thick and tough. At the anterior end is a heavy pedicel of variable length, ranging up to 0.25 mm., the distal extremity of which is irregularly expanded. This "button" is embedded in the integument of the host and anchors the egg firmly in position. Both pedicel and button become black and shriveled after deposition. It is noteworthy that the pedicel mentioned is not represented by any modification in the ovarian egg, which is elongate-oval in form and has the anterior end smoothly rounded. This, and the fact that the pedicel darkens and shrivels quickly after formation, would indicate that it may be formed from secretions of the accessory glands or from material that appears to envelop the anterior end of the ovarian egg, though this point has not been studied. It may be pointed out, also, that the pedicel is situated at the anterior end of the egg, whereas in other pedicellate ichneumonoid eggs the pedicel and its "anchor" are represented by definite structures on the ovarian egg and are situated at the posterior end. As the embryo develops, the paired caudal processes can be seen lying along the mid-ventral line and extending forward to the posterior margin of the head.

The first-instar larvae (Fig. 41*A*, *B*) of the two species present no apparent points of distinction. The body comprises 13 segments, exclusive of the head, and measures 1.2 mm. in length to the base of the caudal processes. The head is heavily sclerotized, slightly broader than long, and bears dorsally a pair of horn-like structures markedly similar to those of the planidia of the Perilampidae. There are four pairs of minute setae dorsally and three pairs ventrally. The mandibles are simple. Each body segment except the last bears a median transverse row of heavy spines dorsally, and these diminish in length caudad. On the first five segments, the rows are continuous across the dorsum, but on those following the row is interrupted medially. The first segment bears two pairs of lateral setae, and the following segments bear one pair. The venter of each of the first eight segments bears a broad band of minute setae, and on each of the following four segments the band is interrupted medially. The caudal segment is bifurcate, and the two tapering, heavily sclerotized prongs are 0.9 mm. in length, diverge at an angle of about 80 deg., and are directed somewhat ventrad. The lobes at the base of the prongs bear numerous robust setae dorsolaterally. The anal opening is ventral on the last segment. There are no spiracles and no visible internal tracheal system.

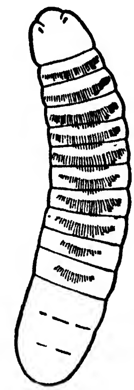


FIG. 42.—A supposed first-instar larva of *Agriotypus armatus* Wlk., found in larvae of *Silo* and *Goera*. (*From Henriksen*, 1922.)

Henriksen describes the supposed first-instar larva of *A. armatus* (Fig. 42) which he states was found internally in *Silo* and *Goëra*. Aside from its occurrence internally, it differs markedly in form from the actual first-instar larva described by Fisher. The body is 1.4 mm. in length, cylindrical, with the caudal end bluntly rounded and lacking the bifurcate process. Certain characters, however, seem to link it with the Agriotypidae, these being the "horn-like" structures on the head and the transverse rows of spines on the dorsum of the body. It seems improbable that this larva can be of *Agriotypus*, but if this proves to be the case it must be the second instar rather than the first.

The second-instar larva of *A. armatus* (Fig. 41*D*) described by Fisher differs from the first in lacking the heavy integumentary spines, and the long bifurcate caudal

process is replaced by a pair of shorter, heavy, opposed hooks. The mandibles are conspicuously toothed. An internal tracheal system is present though there are no spiracles, and the transverse commissures, also, are apparently lacking.

The third and last larval instar is similar to the second, though the caudal hooks are relatively much smaller. The head is quadrate in form, and the mandibles are coarsely dentate. In *A. armatus*, there are said to be no spiracles, whereas nine pairs occur in *A. gracilis*. In view of the conditions under which the mature larva passes the last portion of the stage, in which it is surrounded by air rather than water, open spiracles would seem to be essential.

CHALCIDOIDEA

The superfamily Chalcidoidea includes among its different families probably a majority of all entomophagous insects, and their range in form, habits, host preferences, and host relationships is extremely wide. The bulk of the species are entomophagous in habit, and the phytophagous species are distributed in a number of families. The plant-feeding habit in the superfamily has been reviewed by Gahan (1922) and the species listed which develop in that way. The Agaontidae comprise the fig insects, and the members of the subfamily Idarninae of the Callimomidae are associated with them in an uncertain capacity. Numerous other Callimomidae are seed feeders, as are also many Eurytomidae. The latter family also includes a considerable number of species that form plant galls, and a few species of Eulophidae and a single one of the Encyrtidae are stated to be of similar habit. It is generally accepted that the phytophagous habit is the more primitive in the superfamily and that the parasitic relationship is of more recent origin.

The insect hosts of the parasitic and predaceous members of the superfamily are extremely varied and represent practically all the more common orders, of which the preferred ones are the Lepidoptera, Diptera, Coleoptera, and Homoptera. These groups comprise the bulk of our major crop pests, and their chalcidoid parasites often serve to keep them in check. In biological control work, a considerable number of species have been imported into the different countries and have been successful in reducing the population of the pest species to a noneconomic level.

The host stages attacked are principally the egg and larva, though a smaller number develop in the pupa, and some of those attacking Homoptera may develop in the adults, also. Certain families are sharply restricted in their choice of host groups or host stages. Thus the Mymaridae and Trichogrammatidae develop exclusively in the eggs of various orders, whereas the Eucharidae occur only upon the larvae and pupae of ants. The great majority of Aphelinidae are parasitic in Homoptera, principally the Coccidae, Aphididae, and Aleyrodidae. The parasitic Callimomidae attack mainly the immature stages of gall-making Cecido-

myiidae and Cynipoidea; but the Eulophidae are largely governed by the host habitat, and they attack larvae of several orders that form leaf mines or that bore in stems. The manner of attack shows considerable variation. The larvae that feed upon eggs are usually parasitic internally, but some may be true predators. When attacking larvae or pupae, the parasite may develop either internally or externally, and both habits are commonly found within a single genus. Finally, the adult parasites themselves may be predaceous.

In all probability, the majority of species in the Chalcidoidea are primary parasites, and the known members of the Mymaridae, Trichogrammatidae, Leucospidae, and Eucharidae are exclusively so. Other families have a varying proportion that act as hyperparasites, and some species develop indiscriminately in both roles.

Many modifications in form are found among the eggs and the larval instars of the Chalcidoidea, a majority of which are definitely adaptive in character. Certain of these are common to whole families, whereas others appear apparently independently in widely separated genera and families. Under these circumstances, they cannot be considered to have a phylogenetic significance and are of limited usefulness in determining the taxonomic position of stages not associated with the adult insects. The first comprehensive study of the early stages of the Chalcidoidea, in which an effort was made to arrange the different groups in accordance with their taxonomic position, was that of H. L. Parker (1924).

MYMARIDAE

The family Mymaridae is of cosmopolitan distribution and consists of species of minute size, often only a fraction of 1 mm. in length, with exceptionally long antennae, of which the distal segment is much enlarged in the female and the wings are long, narrow, and fringed with long hairs. A few species, such as *Polynema microptera* Bakk., have the wings much reduced, though of normal form. There are said to be three forms or races of *Prestwichia aquatica* Lubb. (Henriksen, 1922), the typical one having fully winged females and males with rudimentary wings. The second form has the wings rudimentary in both sexes, and in the third the wings of the females are reduced.

All the members of the family, so far as known, are internal parasites in the eggs of other insects, particularly of the Homoptera, but also of the Odonata, Lepidoptera, Coleoptera, Neuroptera, Hemiptera, and Corrodentia (fam. Psocidae). Several have been recorded from Coccidae and Aleyrodidae, but in these instances the exact relationship has not been determined.

Representatives of the family have been successfully utilized in several instances for the control of crop pests. During 1904, a number

of species were introduced into Hawaii from Australia in the attempt to control the sugarcane leafhopper, *Perkinsiella saccharicida* Kirk. Of these, *Anagrus frequens* Perk., *Paranagrus optabilis* Perk., and *P. perforator* Perk. became established and, in conjunction with other parasites, brought about partial control, which was later rendered complete by the introduction of the mirid egg predator, *Cyrtorhinus mundulus* Bredd., from Australia and Fiji in 1920.

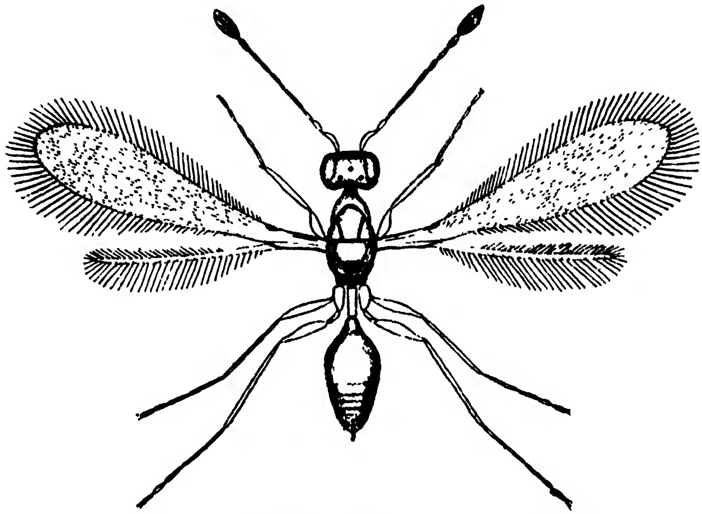


FIG. 43.—The adult female of *Polynema longula* Foerst. (*From Bakkendorf,* 1933–1934.)

Anaphoidea nitens Gir., parasitic in the eggs of the eucalyptus weevil, *Gonipterus scutellarus* Gyll., in Australia, has been utilized against the same host in New Zealand and South Africa and against *G. gibberus* Bsd. in Argentina. Complete control is reported in some sections of South Africa.

BIOLOGY AND HABITS

The Mymaridae are true egg parasites in the sense that they normally attack the host eggs before an appreciable development of the embryo has taken place. In eggs of *Perkinsiella* attacked by *Paranagrus*, development of the embryo is inhibited. *Prestwichia aquatica* is said to oviposit in eggs of any stage of development, but it is not able to mature in those containing advanced embryos. *Anaphes nipponicus* Kuway. limits its attack to *Lema* eggs that are only one to three days old. *Polynema striaticorne* Gir., which produces three successive generations in a single brood of eggs of *Ceresa,* is a conspicuous exception to the above generalization and is able to attack successfully even those containing well-developed embryos (Balduf, 1928*b*).

The great majority of species of the family are solitary in habit. This applies particularly to the dominant genus *Anagrus*, and the only exception in this genus is *A. atomus* L., which, while solitary in the eggs of *Erythroneura pallidifrons* Edw. in England (MacGill, 1934), develops regularly in twos in those of *Tettigonia viridis* L. (Pierre, 1906). From one to seven *Anaphes nipponicus* emerge from each parasitized egg of *Lema oryzae* Kuway., though it is most frequently solitary, and an average of seven *Anaphoidea calendrae* Gahan develop in those of *Calendra* spp. A maximum of 50 *Prestwichia aquatica* has been secured from single eggs of the larger species of *Dytiscus*.

Habits of the Adult.—The genera *Anagrus*, *Caraphractus*, and *Prestwichia* include species in which the adults are of aquatic habit; this is made necessary by the occurrence of the host eggs, in which they develop, beneath the water surface in streams and ponds. Several authors have described the manner of swimming of the adult of *P. aquatica* and its varieties. According to Enock (1898), the middle legs only are used, whereas Henriksen states that the hind legs serve this purpose. Both sexes are capable of swimming, and they are also able to walk on the surface of the water. Heymons (1908) states that adults remained under water for five days without harm. *A. brocheri* Schulz is unable to swim but moves about in the water by walking upon foliage, plant stems, or other objects.

Enock mentions the mating of *P. aquatica* in the eggs of Dytiscidae in which they had developed and prior to the emergence of any of the individuals in the group. Rimsky-Korsakov confirms this observation and states that one male may mate with all the females in turn in the egg. Heymons and Henriksen (1922), however, were unable to verify this habit and saw no indications of mating activity on the part of the males, for all individuals in the egg remained quiescent until one had made an emergence hole, whereupon they escaped one by one.

Adult life is consistently very short, and in a number of species the females are able to deposit eggs immediately after emergence. The reproductive capacity is low, though Balduf mentions that the *P. striaticorne* female is able to deposit 18 to 20 eggs in quick succession, for each of that number of ovarioles in the reproductive system contains one mature egg. Kuwayama (1935) found an average of 26 eggs in the ovaries of gravid females of *Anaphes nipponicus*. The egg production in most species probably does not exceed 100.

In preparation for oviposition, the female of *Polynema striaticorne* searches rapidly over the bark of twigs infested with *Ceresa* eggs, tapping the surface constantly with the tips of the antennae. When an oviposition scar containing living eggs is encountered, she inserts the antennae into the crevice and taps the eggs to determine their suitability. She

then stands astride the crevice, retaining the tips of the antennae in contact with the eggs, brings the ovipositor forward to a perpendicular position, and thrusts it into the top of an egg. Usually all the eggs in the packet, numbering 7 to 12, are attacked at this time.

The species that attack insect eggs deposited upon the surface of foliage experience no difficulty in oviposition, but where these are inserted in leaf tissue or in plant stems a portion may be protected from attack. The female of *Anaphoidea luna* Gir. is able to reach only the few eggs of *H. variabilis* Hbst. that are near the oviposition puncture in fresh alfalfa stems; but she is able to enter dried stems, and all the eggs of the mass are consequently exposed to attack. Among the egg parasites of the sugarcane leafhopper, *Paranagrus optabilis* parasitizes principally the eggs at the base of the mid-rib, whereas *Anagrus frequens* Perk. limits itself mainly to those at the edge of the distal portions of the leaf (Perkins, 1905*e*).

Egg and Larval Development.—A detailed study of the embryological development of a member of the family, given as *Polynema* sp. but stated by several more recent authors to be of the genus *Anagrus*, is presented by Ganin (1869). In this species and in *Prestwichia aquatica* var. *solitaria* R. & T., there is an appreciable growth of the egg during incubation, which amounts in the latter species to an increase in length from 0.22 to 0.38 mm. within 24 hours after deposition.

Little can be said regarding the development of the sacciform first-instar larvae of *Prestwichia* and of several species of *Anagrus*. They lie in the egg fluids and are entirely incapable of movement. Respiration, and possibly a certain intake of food materials also, is by diffusion through the skin. The mymariform first-instar larvae, which occur in practically all other genera, are well-developed and capable of considerable activity. The tail is utilized in moving about in the host egg, and this movement is facilitated by the use of the several rows of long spines on the body segments. This activity is said to disorganize the egg contents.

A conspicuous feature, observable in insect eggs that contain intermediate-stage and nearly mature mymarid larvae, is that the egg contents are in almost constant agitation as a result of the writhing or rotary movements of the parasite larvae. The heavier semisolid contents are thus prevented from settling to the bottom of the egg, and a constant supply of food material is within reach of the mouth. In *Anaphoidea nitens*, these movements persist for three or four days; during this time, one end of the egg becomes filled with a thick yellowish material, presumed to be an excretion of the parasite larva.

In certain families of chalcidoid and serphoid egg parasites, the eggs containing developing parasite larvae are recognizable by a distinctive coloration. This is true of at least some species of Mymaridae,

also, and in several species of *Anagrus* the host eggs containing advanced larvae and pupae are bright red or yellow in color. The body color of the larvae and the remaining portions of the egg fluids are visible through the delicate chorion. Parasitism of *Polynema striaticorne* in the eggs of *Ceresa* results in the deposition of a black pigment in the vitelline membrane, which is a reaction more generally associated with *Trichogramma* parasitism.

Life Cycle.—The majority of species for which information is available have only a single generation each year, which is correlated with the annual cycle of the host. *P. striaticorne,* which has been studied by Balduf, is parasitic in the eggs of various Membracidae, particularly the buffalo treehopper, *Ceresa bubalus* F., and this host has a single annual generation, with the winter passed in the egg stage. The parasite, however, passes through three generations in this one brood of eggs. Other species, having multibrooded hosts, breed without interruption throughout the season, so long as temperature conditions are suitable. *Paranagrus optabilis* produces a generation every three weeks under subtropical conditions, *Anaphes nipponicus* completes its cycle in 8 to 13 days and has five or six generations each year, *Anaphoidea nitens* requires 17 to 22 days to complete its cycle, and *Anagrus atomus* L. requires a minimum of 16 days.

The duration of the egg stage is relatively short, as the larva of *Anaphoidea calendrae* was found less than six hours after oviposition by the parent female, and in *A. nitens* hatching takes place in one to two days. In the latter species, the larval and pupal stages require 6 to 8 and 10 to 12 days, respectively. The hibernation stage is known for several species of *Polynema, Ooctonus,* and *Lymnaenon,* and in each case the first-larval instar is found in the host eggs during the winter. *Anagrus armatus* var. *nigriventris* Gir. hibernates in the half-grown "histriobdellid" form (Armstrong, 1936).

Sex Ratio and Parthenogenesis.—Information regarding the sex ratio of the Mymaridae is available for only a small number of species. In *P. aquatica,* the females are said to outnumber the males 20 to 1, and in *Anaphes nipponicus, Anagrus incarnatus,* and *A. armatus* var. *nigriventris* by 2 or 3 to 1. According to Mossop (1929), the ratio in *Anaphoidea nitens* Gir. varies appreciably under field conditions, but the females consistently predominate, the highest ratio being about 3 to 1. In *A. calendrae* (Satterthwait, 1931), which produces an average of seven individuals in each host egg, 72.5 per cent of the "broods" contain only a single male and only 15 per cent contain more than one. In contrast to this, the males predominate in the ratio of more than 3 to 1 in *Polynema striaticorne.* Collections of the latter species covering the entire season showed them to outnumber the females by 3 to 1.

Unisexual reproduction is the normal habit of *Anagrus atomus, A. frequens, Paranagrus optabilis, P. perforator*, and *Polynema euchariformis* Hal. Males have been found occasionally, however, in each of these species with the exception of the last. Other species that are normally bisexual are able to reproduce parthenogenetically, in which case all progeny are males.

IMMATURE STAGES

There is little variation in egg form within the family. The main body of the egg is ellipsoidal, ovoid, or spindle-shaped, with a slender tapering peduncle at the anterior end ranging in length from one-tenth that of the egg body in *Anaphoidea nitens* and *Caraphractus* to equal its length in *Polynema striaticorne* (Fig. 44*A*). The ovarian egg is practically identical with the laid egg. These eggs are exceedingly minute, ranging from 0.06 mm. in length in *Anagrus atomus* to 0.25 mm. in *P. striaticorne*.

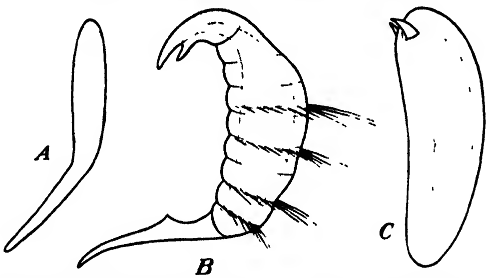


FIG. 44.—Immature stages of *Polynema striaticorne* Gir. *A*, the egg; *B*, first-instar larva, *C*, mature larva. (*From Balduf*, 1928.)

A great deal of confusion exists regarding the larval forms of the Mymaridae. This is primarily due to the exceedingly minute size of the early stages combined with the lack, in the instars following the first, of heavily sclerotized or indurated structures of fixed form. Often several species have been involved in the descriptions of the instars of what was supposedly a single species. This was the case in the account given by Ayers (1884) of *Teleas* sp., a scelionid parasite in the eggs of *Oecanthus* in the United States. His figures 2.3, 8, 12, and 13, of plate 24, are undoubtedly of *Polynema* (Fig. 46*A*), which is stated by E. W. Wheeler (1923) to be *P. bifasciatipenne* Gir. The *Polynema* sp. figured by Ganin is stated by Bakkendorf to be *Anagrus*, probably *A. incarnatus* Hal., though Henriksen believes it to be *A. subfuscus* Foerst.

There are two general types of first-instar larvae. The first of these is oblong or flask-shaped, of the sacciform type, and occurs in the several species of *Anagrus* that have been studied and in *Prestwichia aquatica*. The body is merely a bag, without segmentation, and lacks any distinguishing characters. Bakkendorf (1934) figures a somewhat intermediate form between this and the next, in what are considered to be first-instar larvae of *Allaptus minimus* Hal. and *Lymnaenon effusi* Bakk. (Fig. 46*B*). These are rather spindle-shaped, with indications of segmentation, and have the caudal segment attenuated and tapering to a point. There is no distinct tail structure, nor are there spines or setae.

The second and more common form of the first-instar larva is designated as mymariform and occurs in the described species of *Polynema, Anaphes, Ooctonus*, and *Anaphoidea*. The head is large, drawn out into a curved median conical process, with a second smaller process beneath it, representing the mouth. The thorax and abdo-

men consist of six to eight segments, often indistinguishable, with transverse rings of long hairs, which are most numerous upon the dorsum. The dorsal spines of *P. euchariformis* (Fig. 45*A*) and *Anaphoidea nitens* are exceptionally long and heavy. The caudal end of the body bears a long, curved or abruptly bent process, often equal to the body in length, which, in some species, is compressed laterally into blade-like form and bears a single large tooth or one or more smaller paired teeth on the ventral margin. Clark (1931) describes two distinct mymariform instars in *A. nitens;* the first of these has the tail slender and bent at right angles twice, first ventrally and then dorsally, whereas in the second form it is constricted and toothed at several points (Fig. 46*C*). This is highly improbable, and the two forms doubtless represent either two species or different ages of the first instar of the same species. In size the first-instar larvae of the Mymaridae are small and range from 0.1 to 0.3 mm. in total length at the time of hatching.

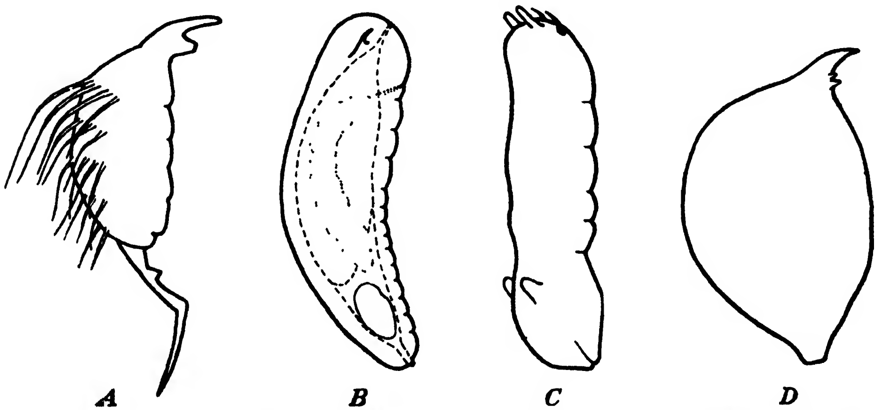


FIG. 45.—Immature stages of the Mymaridae. *A*, first-instar larva of *Polynema euchariformis* Hal.; *B*, second-instar larva *P. ovulorum* Hal.; *C*, "histriobdellid" second-instar larva of *Anagrus incarnatus* Hal.; *D*, second-instar larva of *Polynema pusillus* Hal. (*From Bakkendorf*, 1933–1934.)

The number of larval instars following the first is very uncertain. Several authors assert that there are only the first and the mature forms, though in most species there are said to be three. Balduf describes four in *Polynema striaticorne*.

The second-instar larva of *Anagrus* is of distinctive form and has been designated as "histriobdellid" by Ganin, who first observed and described it. This larva (Fig. 45*C*) is cylindrical in form and is divided by constrictions into six segments, of which the first and last are largest. The head bears a pair of large, conical or cylindrical fleshy processes lateroventrally, which are said to be the antennae, and the extruded mandibles, which are long, slender, and curved, lie parallel to each other. The last segment bears a pair of large ear-like organs, of unknown function, lateroventrally. This type of larva has thus far been associated only with the sacciform first-instar larva and is not known in any species having mymariform larvae.

The second-instar larvae of *Prestwichia*, *Anaphoidea*, and *Polynema* (Fig. 45*B*, *D*) have few distinguishing characters except for the relatively large extruded mandibles, which are somewhat fleshy. The body is bag-like, without segmentation, and lacks appendages, spines, or setae.

The mature larvae of *Anagrus* and *Paranagrus* are similar to the histriobdellid form except that the ear-like processes of the last segment are lacking and the mandi-

bles and antennal processes are much reduced in size. Those of *Polynema* (Fig. 44*C*), *Prestwichia*, *Anaphes*, and *Anaphoidia* are indistinctly segmented and, aside from the large extruded mandibles, have no recognizable characters. The larva of *Erythmelus goochi* Enock appears to be intermediate in form between *Anagrus* and the above genera.

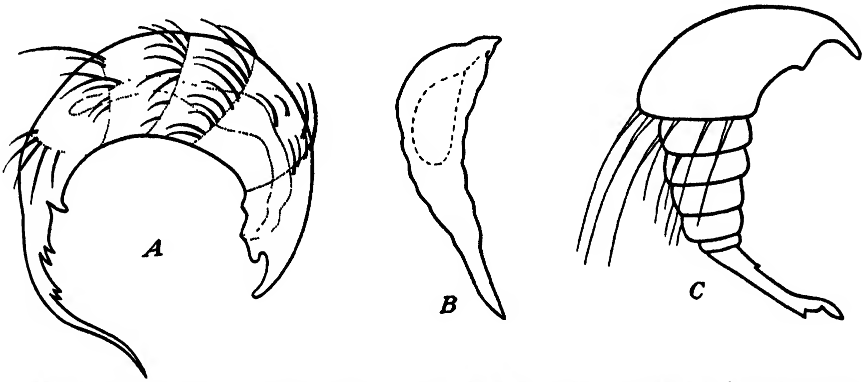


FIG. 46.—Larvae of the Mymaridae. *A*, first-instar larva of *Polynema bifasciatipenne* Gir. (*from Ayers*, 1884); *B*, first-instar larva of *Lymnaenon effusi* Bakk. (*from Bakkendorf*, 1933–34)· *C*, presumed second-instar larva of *Anaphoidea nitens* Gir. (*from Clark*, 1931).

In no species is there any indication of an internal tracheal system or spiracles in any of the larval instars.

TRICHOGRAMMATIDAE

The family is cosmopolitan in distribution and comprises a relatively small number of genera, the most common of which is *Trichogramma*. All species, so far as known, are primary internal parasites of the eggs of other insects. The greatest diversity in hosts is revealed in *Trichogramma*. For *T. evanescens* Westw. (*minutum* Riley) alone, Martin (1928) refers to more than 150 host species, representing seven orders; Megaloptera, Lepidoptera, Coleoptera, Hymenoptera, Neuroptera, Diptera, and Hemiptera, the great majority of which are Lepidoptera. Though it is probable that several species are represented under one name, yet an exceptional range in host preferences is still illustrated. Schread and Garman (1933) refer to more than 215 hosts of the genus.

In a recent study of the North American representatives of the genus, Flanders[1] (1935*c*, '38*b*) groups them into three species, largely on the

[1] The names assigned by Flanders are used here chiefly for convenience in discussion, for a considerable portion of the biological data on the genus is by that author. The determination of species on the basis of habitat only, in the absence of morphological characters to distinguish them, is open to several objections. These names proposed for the North American species are not at present accepted by specialists in the family.

basis of the environment that they inhabit. As a result of this difference in habitat, he finds that each species has a different host complex, and the three are rarely found associated. *T. embryophagum* Htg. (*pretiosa* Riley) occurs in arboreal habitats, *T. evanescens* Westw. (*minutum* Riley) under field conditions, and *T. semblidis* Aur. in marsh habitats. Other less common genera of the family are *Chaetostricha*, recorded from the eggs of Lepidoptera, Coleoptera, Hymenoptera, and Hemiptera, *Oligosita* from coleopterous and hemipterous eggs, *Ophioneurus* and *Poropoea* in coleopterous eggs, *Ufens* in cicadellid eggs, and *Lathromeris* in those of *Orthoptera*.

The various members of the family, particularly of the genus *Trichogramma*, are often of considerable value in the natural control of their hosts. In many cases, a field parasitization of 90 per cent or more has been recorded, though this almost invariably occurs relatively late in the season and consequently its value against multibrooded species, or those which cause their greatest injury during the spring and early summer, is reduced. These parasite species suffer a very high winter mortality, due primarily to lack of host eggs in which to develop, and consequently they require a number of generations to build up the population to an effective level the following season. Also, the habits of the adult females are such that a high percentage of parasitization can be attained only in a high host-egg population. One factor that operates against the attainment of a high parasitization in eggs of pest species which deposit them in masses is that the parasite is usually limited to attack upon the topmost layer.

The first attempt to rear *Trichogramma* on a large scale and to utilize it in the biological control of a crop pest was by Radetzky (1912), who imported *T. semblidis* (*Pentarthron carpocapsae* Ashm.) into Taschkent for the control of the codling moth. The parasite was reared in the laboratory in the eggs of the browntail moth. Since that time, extended experiments in the biological control of a number of crop pests, particularly the sugarcane moth borer, certain lepidopterous rice borers, and the codling moth, have been undertaken in many countries. Most of these have resulted negatively, though a definite reduction in caneborer population has been claimed in several tropical countries.

BIOLOGY AND HABITS

Habits of the Adult.—In effecting emergence, the adult bites away a hole in the chorion of the egg in which it has developed. Faure (1926) states that all individuals of *Trichogramma* developing in the egg of *Ascia* leave it through a single emergence hole. Emergence takes place largely during the early morning, and the females are able to oviposit the same day.

In the act of oviposition in large host eggs, the parasite stands upon it and inserts the ovipositor perpendicularly, whereas with small eggs this is accomplished by a backward thrust. In *Poropoea*, which attacks curculionid eggs contained in leaf rolls, the ovipositor is inserted through one end of the roll. The female of several species of *Trichogramma* feed upon the fluids exuding from the ovipositor puncture in the host egg.

Ferriere (1926*a*) calls attention to the first apparent instance of phoresy in a member of the family. Fourteen females of *Oligosita xiphidii* Ferr. were found clinging to the hind wings of a tettigoniid, *Xiphidion longipenne* de Haan, in Java. The host preferences of *O.*

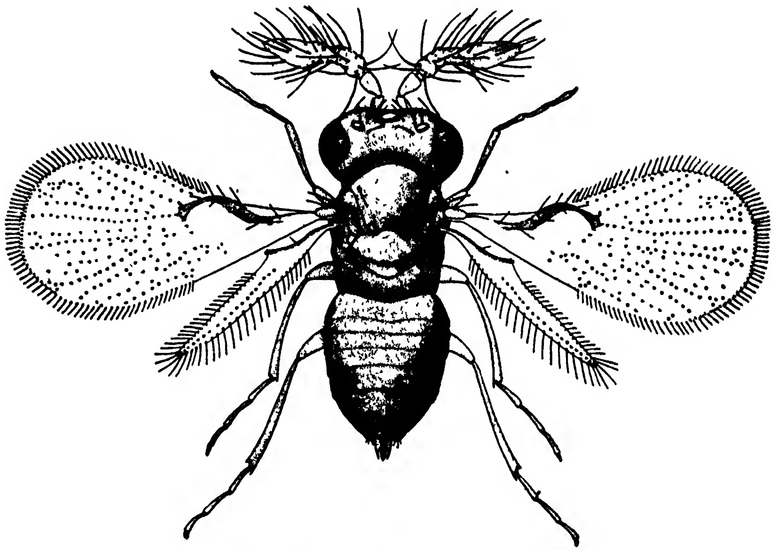


FIG. 47.—The adult male of *Trichogramma minutum* Riley. (*Drawing by Carla Henrich.*)

xiphidii have not yet been determined, but it is assumed that the females attached themselves to *Xiphidion* in order to gain access to their eggs immediately after deposition.

It has been determined that the ability of *Trichogramma* females to penetrate the chorion of different eggs increases with an increase in size of the females themselves. Large females are able successfully to attack large host eggs having a thick chorion, whereas the small individuals are restricted to eggs having a light chorion. This physical limitation explains, in part at least, the different results obtained by various investigators using the same parasite species or race, but eggs of different host species in which to rear them. Tothill *et al.* conclude that, where a choice of hosts is presented, the determining factor in selection is the relative penetrability of the chorion of the egg.

Most species of *Trichogramma* are able to oviposit successfully in host eggs of almost any stage of development. However, *T. evanescens* is stated to prefer freshly laid eggs of the gypsy moth and the cabbage butterfly, although those containing well-developed embryos and even dead eggs may be successfully attacked. Several authors state that oviposition, with successful development, is possible in host eggs in which the embryo is fully mature and on the point of hatching. Tothill *et al.* (1930) found that in *Chilo*, *Schoenobius*, and other rice borers the embryo is killed by the insertion of the ovipositor of *T. nana* Zehnt., whether or not an egg is deposited. Martin (1928) and Peterson (1930) mention that oviposition by *T. evanescens* inhibits further embryonic development. Several eggs may be deposited at one insertion of the ovipositor.

The stimuli that operate upon the female at the time of oviposition appear to be rather simple and lead the female into numerous errors of instinct, resulting in oviposition or attempted oviposition in numerous "false hosts" in which development cannot take place. Holloway (1912) describes oviposition by *T. evanescens* females in globules of partly dried sap of the okra plant which had formed a surface film. This gave the globules a superficial resemblance to host eggs. The detailed examination of an object with the antennae is apparently for the purpose of locating a suitable point for the insertion of the ovipositor. Salt (1935) describes attempted insertion of the ovipositor in objects such as bits of glass, globules of mercury, plant seeds, etc., and in insect eggs in which development to maturity is impossible. He concludes that the principal criterion utilized by the female in her choice of hosts is size. Marchal (1936) likewise records oviposition of the same species in globules of sap of *Hibiscus*. He disagrees with Salt as to the dominant influence of size governing host selection, for surrounding conditions, in conjunction with the senses of the female, certain of which it is impossible to judge, all enter into the problem. Very probably, these so-called errors of instinct occur much less frequently under natural conditions than in the confined quarters necessitated by experimental procedure.

Experiments conducted by several investigators have indicated that oviposition is random and that the female is incapable of determining prior attack upon the host egg or at least that she disregards it in oviposition. Salt (1934), however, has found that this conclusion is erroneous for *T. evanescens* and that the female avoids oviposition in host eggs already parasitized either by herself or by another female. In case an adequate supply of unparasitized eggs is not available, she will withhold deposition for a time rather than place her eggs in hosts already attacked. When forced to deposit more than the normal number of eggs in a limited number of host eggs, she will choose the larger hosts to receive the surplus eggs. Superparasitization occurs in a much smaller percentage of eggs

than would be expected from random oviposition. To test this point, a series of 10 females were confined for eight hours with 10 host eggs each, and a total of 138 eggs were deposited during this period. By the laws of chance, only 34.7 per cent of these hosts should have received only one egg, whereas actually 69 per cent contained only one. Restraint in oviposition was also indicated, for a check series of an equal number of females provided with an ample supply of hosts deposited 225 eggs during the same period of time. Later investigations (Salt, 1937*a*) upon the senses involved in selective oviposition revealed that sight, hearing, and touch play no part in the choice of host eggs, but that a chemical sense is employed. The female is able to recognize the external odor of another parasite of its own species that previously had walked upon or stung the egg. If the egg is then washed, she will attack it without hesitation, though the ovipositor is quickly withdrawn if parasitization had previously been effected.

There is a considerable difference in the reproductive capacity of *Trichogramma* as recorded by various authors. *T. embryophagum* is stated by Schread and Garman to deposit a maximum of 29 eggs, whereas 50 were secured from *T. evanescens.* The former is said to be less prolific in small eggs and more so in large eggs than *T. evanescens.* Peterson (1930) secured a much higher rate of reproduction, finding that one female of the latter species produced 131 progeny. Salt secured a total of 225 eggs from a series of 10 females provided with an adequate supply of host eggs.

In a comparative study of reproduction in two common species of the genus in North America, presumably *T. evanescens* and *T. embryophagum,* Bowen (1936) found that the mean reproductive capacity of the former was 37 as compared with 62 for the latter. He confirmed the conclusions of previous workers that the two do not interbreed.

The subject of the longevity and productivity of the adults of *T. evanescens* under varying conditions of temperature and humidity has recently been investigated by Lund (1938). The average length of adult life was found to be approximately six days at a temperature of 25°C. Forty per cent of the eggs were deposited within 12 hours after emergence of the adult parasite, and 76 per cent within two days. The withholding of host eggs until two or three days after emergence materially reduced the productivity of the females, though it did not affect their longevity. Females that remained unmated throughout the oviposition period produced an appreciably greater number of eggs than did the mated females. This is the direct opposite of the known oviposition habits of most other parasitic Hymenoptera.

Dimorphism of Adults.—A pronounced seasonal dimorphism occurs in *T. cacoeciae* Marchal, parasitic in the eggs of *Cacoecia roseana* L. in

France, which has been studied in great detail by Marchal (1927, '36). This host has a single generation each year, with the eggs deposited during July and persisting in this stage until the following spring. Two generations of *T. cacoeciae* develop in these eggs. The adults of the overwintering generation, which are rather dark in color and possess vestigial wings, emerge in late March or April. The second generation, being upon these same overwintering eggs, must develop in those in which embryonic development is considerably advanced. The adults resulting from this generation are light-colored and possess normal wings. The adults from the overwintering generation in *Mamestra* eggs, after a number of generations of the normal winged form in that host during the one season, likewise show a marked tendency toward micropterism.

Salt (1937*b*) has made an interesting study of the dimorphic *T. semblidis*, parasitic in the eggs of *Sialis* in England. All males that developed in these eggs were found to be wingless. The females were mated with these apterous males, and the following generation was produced in grain-moth eggs. Quite surprisingly, the males of this brood were fully winged. Such an influence of the host upon the form of the parasite attacking it was quite unexpected. The two forms of male are quite distinct, and intermediates do not occur. Other parts of the body as well as the wings are radically changed. This dimorphism of the males is considered to be comparable in some respects to that of the females in the Cynipoidae and in some social Hymenoptera. The changes brought about likewise have a nutritional basis, but in quality rather than quantity. Winged males from *Sitotroga* and *Ephestia* eggs are smaller than the apterous males from *Sialis*.

Martin (1928) refers to the appearance of vestigial-winged forms in *T. semblidis* (*T. minutum*) developing in the eggs of *Sialis infumata* Newm. in North America. All males and a portion of the females were of this form. The males of this species are said to be commonly dimorphic.

Temperature has a considerable influence upon the coloration of the adults. Flanders (1931), in studying the various races of *T. evanescens*, found the general yellow body color to be obscured by dark pigments when development takes place at low temperatures.

Development of the Immature Stages.—Little need be said regarding development of the egg and following immature stages of *Trichogramma*. There is a considerable increase in volume of the eggs during incubation. The larvae lie immobile in the egg fluids, gradually consume them completely, and pupate *in situ*. In *Poropoea* and other genera having mymariform larvae, the younger stages are more active and are apparently able to disorganize the egg contents somewhat by lashing movements of the tail.

Oligosita utilis Kow. differs from other species of the family in voiding the meconium at the end of the larval period rather than retaining it until after adult emergence. Flanders states that the pupal skin and the last larval exuviae, also, are scraped off by the adult of *Trichogramma* as it emerges.

In *Oligosita* and others that attack flat eggs, the pupa normally lies upon its back, a position that facilitates adult emergence.

Trichogramma parasitism is much more quickly apparent and induces more noticeable physiological changes than that of most other groups of egg parasites. In *T. nana* (Tothill *et al.*, 1930), the area surrounding the point of puncture in the *Artona* egg becomes blackened in two to three days after attack. Shortly thereafter, black streaks and patches appear in the same general area and extend down the side of the egg. Finally, this color change becomes uniform and complete over the entire egg; dissections show that it is due to a deposit of minute, dark granules on the inside of the chorion. Faure (1926), in discussing *T. evanescens* as a parasite of *Ascia* eggs, states that this color change occurs in the vitelline membrane. Flanders found that the discoloration of the vitelline membrane takes place during the prepupal stage of the parasite. This black lining of the egg remains after the emergence of the parasite; in the case of eggs having a translucent chorion, it serves as a ready means of distinguishing parasitism by *Trichogramma* from that of several other parasite groups. Coleopterous eggs parasitized by *Poropoea* become reddish rather than black.

The number of individuals that are produced in each host egg varies directly with the volume of the egg, and a sufficient number of parasite eggs is usually deposited to ensure complete consumption of the contents by the developing larvae. *Trichogramma* is normally solitary in *Sitotroga* eggs. Flanders (1935*a*) found that 1 to 10 *T. evanescens* develop in each egg of *Estigmene acraea* Drury and that, irrespective of the number of individuals involved, the total mass of adults from one egg is nearly constant. The same author records the development of 50 to 75 individuals in each egg of *Pachysphinx*, and up to 69 of *Trichogramma* sp. from the Philippine Islands have been secured by Shibuya and Yamashita from eggs of *Dendrolimus spectabilis* Butl. in Japan.

Barber (1937) has made a study of several thousand adults of *T. evanescens* that emerged from eggs of the corn ear worm. The population in each egg ranged from one to five. In relative volume the smallest males were only one twenty-fifth the size of the largest, and the smallest females one-fortieth the size of the largest female. There is, consequently, a wide range in the quantitative food requirements of the individuals of this species.

Life Cycle.—The cycle of the majority of species of the family, from egg to adult, is exceedingly short. For *Trichogramma*, this is 7 to 10 days at summer temperatures. Flanders found that in *T. evanescens*, under conditions that yielded adults 8 days after oviposition, incubation of the egg was complete in 22 hours and larval feeding in only 26 hours. Other workers have reported 3 to 4 days as the duration of the larval feeding period. Lund (1934) found that the optimum conditions for development of *T. evanescens* is 32°C. and 100 per cent relative humidity. Salt states that the feeding period is primarily one of ingestion only and that digestion follows more leisurely.

Generation after generation is produced without interruption so long as suitable host eggs are available and temperature and humidity conditions remain favorable. An exception to this generalization is the *Trichogramma* reared by Marchal from the eggs of *Cacoecia* in France. This species produces only two generations each year, a limitation imposed by the annual cycle of the host. This seasonal cycle is not a fixed attribute of the species itself, as was demonstrated by the rearing of seven to nine generations in the eggs of *Mamestra* during one season under laboratory conditions. Embryonic development of *Mamestra* is complete in a short time, and the cycle of the parasite is accordingly expedited. The prolongation of the cycle in the fresh eggs of *Cacoecia* is correlated with the less rapid development of the embryo of the host. The larval diapause is induced by physicochemical influences, particularly those affecting the enveloping membranes. *Poropoea stollwercki*, likewise, has only two generations in the eggs of *Attelabus* in Italy.

The cycles of other genera are usually much longer than that of *Trichogramma*. *Oligosita utilis* has a minimum cycle of 42 days at 29.4°C. in Fiji, of which about 33 hours are required for incubation of the egg, three to five weeks for larval development, and three weeks for the pupal period. The actual feeding period of the larva, however, covers only a few days. According to Silvestri (1916), *Poropoea stollwercki* Foerst. requires 14 to 15 days for the early summer generation. Bakkendorf states that there is probably only a single annual generation of *Chaetostricha pulchra* Kryg. in the eggs of *Tettigonia* and that larval development is complete in one month. In contrast to this is the very short cycle of 7 days recorded for *C. mukerjii* Mani in the eggs of *Bruchus quadrimaculatus* F. in India (Mukerji and Bhuya, 1936).

The hibernation habit has not been conclusively demonstrated in any species of *Trichogramma*, though it is quite certain that the adults do not persist through the winter. So far as known, there is no obligatory diapause, except such as may be imposed by the host, as in *T. cacoeciae*, and development of the immature stages, as well as activity of the

adults, takes place whenever temperature conditions permit. This occurs, in some forms at least, at exceptionally low levels. At the latitude of Tokyo, Japan, adults were seen to emerge and oviposit during February; all immature stages could consequently be found throughout the winter. Under more severe conditions, only the mature larva can be found during this period.

In *P. stollwercki*, which has only two generations, the mature larvae persist in the host egg within the leaf roll from June until the following spring. *Chaetostricha and Ophioneurus*, which have only one to three generations in temperate regions, have the same hibernation habit, and there appears to be a true diapause in the mature larval stage.

Sex Ratio and Parthenogenesis.—The sex ratios of the American races of *T. evanescens* and *T. embryophagum* are approximately 2 to 1 and 4 to 1, respectively, the females predominating. This ratio, however, may be upset by abnormal temperature and humidity conditions. Schread and Garman (1934) found that refrigeration of mature larvae at 8.3°C. or below resulted in a preponderance of males in the following generation. Flanders (1935*a*) determined that *T. evanescens* is always of the female sex when developing from a solitary egg in an *Estigmene* egg, whereas if three mature in each host, which is a more normal condition, the "brood" usually consists of two females and one male. Jones (1937) determined that the ratio in field-collected material of *T. lutea* Gir. was approximately 2 to 1 and that, as in *T. evanescens*, a solitary individual is of the female sex, whereas if two are produced in the host egg they are usually of opposite sexes. With a greater number, there is usually only a single male in the group. Salt, using host eggs of smaller size, found that the proportion of males increased directly with the extent of superparasitization, for that sex dominates when in competition with the females.

Taylor (1937) mentions that *Oligosita utilis* normally produces three or four individuals in each egg of *Promecotheca*. A single male is usually present in each group, and the normal sex ratio is approximately 2.5 to 1.

Unisexual reproduction is apparently normal in several geographic races or strains of the more widely distributed species, such as *T. evanescens* and *T. embryophagum*. It occurs in *T. cacoeciae* and in one race of *T. fasciatum* in Europe; but in *T. flavum* Ashm., discussed by Marchal as a form of the first-named species that develops in *Mamestra* eggs, an occasional male is produced. In the laboratory cultures of *T. cacoeciae*, the first male appeared in the thirteenth generation and several additional in the twenty-sixth and twenty-seventh generations. The latter mated normally, and all progeny were females. Hase (1925), in his work on an undetermined species of the genus, found that virgin females produced approximately equal numbers of male and female progeny. The true

taxonomic position of these various supposed species, races, and strains is so confused at the present time as to render a comparison of experimental results exceedingly difficult.

Marchal reports the occurrence of both bisexual and unisexual strains in the supposed *T. evanescens* reared from *Sialis* eggs in France; but this is at variance with the results secured by Salt (1938) with a species from eggs of the same host in England, but that he considers to be *T. semblidis*. All progeny from virgin females were males.

IMMATURE STAGES

The egg forms of very few species of the family are known. Those of several *Trichogramma* are somewhat elongate, with the middle portion distinctly expanded, and both ends are smoothly rounded (Fig. 48*A*). The egg of *Oligosita utilis* Kow. is of similar form, though with a short, heavy peduncle at one end. In *Poropoea stoll-*

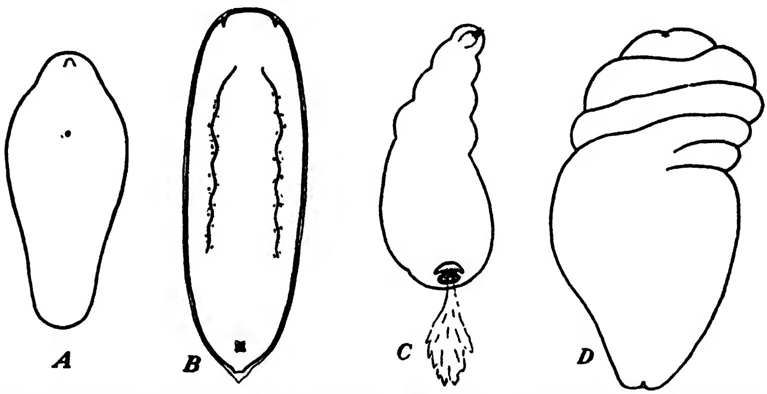


Fig. 48.—Immature stages of *Trichogramma*. *A*, egg; *B–D*, first- and second-instar larvae and prepupa. (*From Flanders*, 1937.)

wercki (Fig. 49*A*), the main body is 0.5 mm. in length, elongate and irregularly curved, and it bears a slender peduncle at the anterior end. The narrower posterior portion presents a somewhat ringed appearance. The egg of *P. defilippii* Rond. is similar, though the peduncle is shorter and more delicate. In *Chaetostricha pulchra*, figured by Bakkendorf (1934), the main egg body is cylindrical, and the anterior peduncle, which is half as long, is set at an angle with the main axis of the egg.

There are two distinct types of first-instar larva, the first of which is sacciform, almost globular or cylindrical, and lacks sensory and integumentary setae and other external characters. The mandibles are minute but distinct. Those of *Trichogramma* (Fig. 48*B*), *Chaetostricha*, and *Oligosita* are of this type. The second is much more highly specialized, being mymariform, with the head and thorax appreciably larger than the abdomen, the segmentation distinct, the caudal segment drawn out into a tail, and the thorax and abdominal segments bear long setae. This type occurs in *Poropoea* and *Ophioneurus*. The first-instar larva of *P. stollwercki* (Fig. 49*B*), as described by Silvestri, is 0.28 mm. in length, with the head and thorax exceptionally large, and the abdomen consists of six ring-like segments and a seventh that is curved ventrally and extended into a point. There are 16 to 18 long, slender setae in a transverse row at the posterior margin of the thorax, situated dorsally and extending

to the lateral margins. All abdominal segments except the last bear a smaller number of these setae dorsally near the anterior margins. The larva of *Ophioneurus signatus* Ratz. (Fig. 50), described by Bakkendorf (1934), has a distinct head; but the thorax

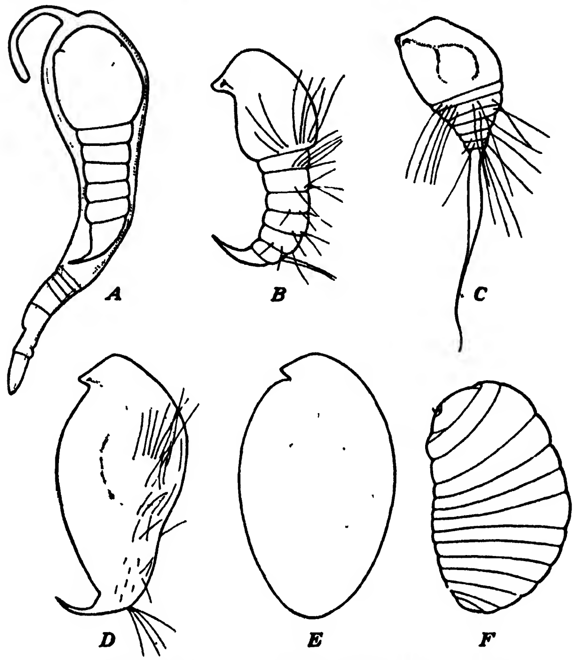


FIG. 49.—The immature stages of *Poropoea stollwercki* Foerst. *A*, fully developed embryo within the egg; *B–F*, first- to fifth-instar larvae. (*From Silvestri*, 1916.)

and abdomen are unsegmented, almost spherical, and the last segment is produced into a slender, curved tail which bears a tooth at the mid-ventral margin. In addition, there is a long, heavy process or spine arising dorsally slightly in front of the base of the tail.

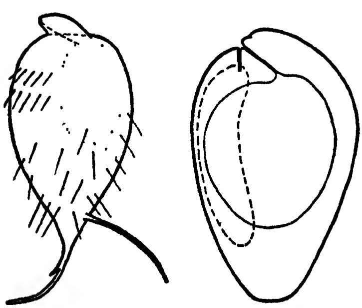


FIG. 50.—First (at left) and second instar larvae of *Ophioneurus signatus* Ratz. (*From Bakkendorf*, 1933–1934.)

There is considerable disagreement as to the number of larval instars in the family. Taylor states that there is only one in *Oligosita utilis*, and Bakkendorf was unable to find evidence of intermediate molts in *Chaetostricha pulchra*. Flanders describes three instars in *Trichogramma*, and Silvestri records five for *Poropoea stollwercki*, though here, also, the evidence of a corresponding number of molts is incomplete.

The second instar of *Trichogramma* (Fig. 48*C*) is somewhat elongate and tapers anteriorly, and the segmentation is indicated only on the anterior half of the body. The mandibles are extruded and only slightly curved. The presumed second-instar larva of *P. stollwercki* (Fig. 49*C*) is still mymariform, with the abdomen further reduced, and the tail exceeds the body in length. It appears more probable that this larva is still of the first instar rather than a distinct second.

Even the third instar as figured (Fig. 49*D*) is identical with the first except for the elimination of the segmental lines, possibly due to an increase in volume through feeding.

The mature larvae of all genera are of similar form, being robust, more or less distinctly segmented, and without spines or setae. The mandibles are elongate and extruded and lie parallel to each other. They are immovable and consequently not used in feeding, though they may serve to lacerate the remaining embryonic tissues in the host egg. Several authors emphasize the complete lack of a tracheal system in the larvae of *Trichogramma*, and it has not been mentioned in other genera.

ELASMIDAE

The family Elasmidae is a comparatively small group, represented most commonly by the genus *Elasmus*. The available host records indicate that the species of this genus are mainly either primary external

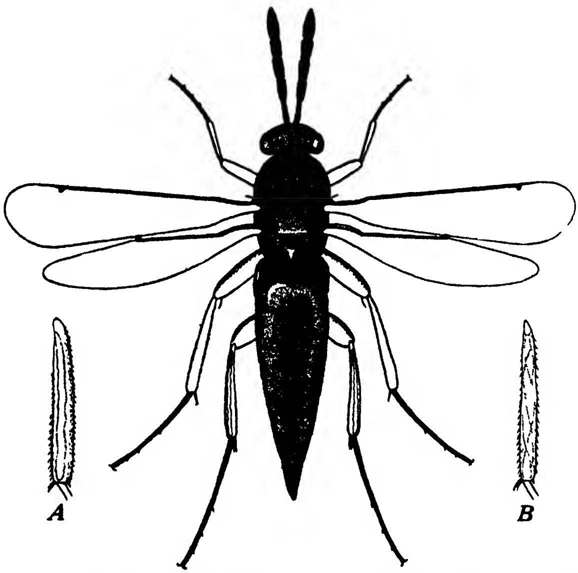


Fig. 51.—The adult female of *Elasmus* sp. *A*, the tibia of a hind leg, showing the linear arrangement of the spines; and *B*, the intersecting lines of spines on the tibia of another species of the genus. (*Original.*)

parasites of the larvae of Lepidoptera or hyperparasites upon them through various Hymenoptera, particularly the Ichneumonidae and the Braconidae. Some species develop regularly in both roles. Most commonly, the hosts attacked are within a web, larval case, or cocoon. Very few species are sufficiently abundant to be of any importance in the control of their hosts.

The genera *Euryischia* and *Myiocnema* differ markedly in their host preferences from the remainder of the family and are considered to represent a connecting link with the Aphelinidae. *Euryischia lestophoni* Riley is recorded from Australia as a hyperparasite of *Icerya purchasi*

Mask. through *Cryptochaetum*, whereas *Myiocnema comperei* Ashm., also from Australia, has been reared from *Saissetia oleae* Bern. though its exact status has not been determined (Smith and Compere, 1928). *E. inopinata* Silv. has been reared from dipterous larvae, possibly Syrphidae, in Sicily.

The adults of the family, at least those of the genus *Elasmus*, are distinctive in appearance. Many may be readily recognized by the compressed, triangular form of the body and abdomen and, in some species, by the arrangement of the setae of the hind tibiae in parallel lines or crossing to form diamond-shaped "cells" (Fig. 51).

BIOLOGY AND HABITS

Relatively few biological studies have been made upon members of this family, the only extended accounts being by Ramachandra Rao and Cherian (1927) upon *Elasmus nephantidis* Roh., parasitic upon the coconut caterpillar, *Nephantis serinopa* Meyr., in India and by Taylor (1937) upon *E. hispidarum* Ferr., which attacks several species of coconut leaf miners of the coleopterous genus *Promecotheca* in Fiji.

The female of *E. nephantidis* makes a close examination of the galleries of silk and frass formed by the host and apparently restricts her oviposition to those individuals which have just spun the cocoon and are in the quiescent prepupal condition. She pierces the wall of the cocoon with the ovipositor, stings the caterpillar, and then drops 10 to 20 eggs near the body. These hatch within one day, and larval feeding is complete about four days later. The mature larvae then congregate in one corner of the cocoon, cast their meconia, and pupate.

The habits of *E. hispidarum* do not differ greatly from those of *E. nephantidis*, though all stages of the active larva, rather than the prepupa of the host, are attacked. In oviposition, the underside of the coconut leaf is pierced by the ovipositor and the larva stung into permanent immobility, and the eggs are then deposited in an irregular group within the mine. The number deposited appears to vary directly with the size of the host individual. Usually, only a single egg is laid in the mine of a first-instar larva, whereas those of the third-instar larvae receive 6 to 18. The latter is the maximum number that can develop to maturity upon a single host. The young larvae wander about the mine in search of the host and die within 30 hours if it is not found. The host larva dies within 12 hours after the beginning of feeding by the parasites. The pupa of the parasite is attached at its posterior end to the wall of the mine by the meconium and the last larval exuviae, the latter being in the form of a thin, twisted thread.

The pupae of *Elasmus* sp., which is parasitic upon bagworm larvae in Japan, are likewise attached by means of the meconium and exuviae,

but they are arranged in a ring about the inside of the case. Mating takes place immediately after adult emergence, and a gestation period of two to three days elapses before the beginning of oviposition.

The life cycles of the Elasmidae appear to be consistently very short; development from deposition of the eggs to the emergence of the adults requires 10 to 16 days for *E. nephantidis* and an average of 14.5 days for *E. hispidarum* at a mean temperature of 29°C.

The reproductive capacity is relatively low; *E. hispidarum* was found to deposit only approximately 50 eggs during a period of one to two months, and the same number is produced by *E. nephantidis* during a considerably shorter life. Voukassovitch (1932*c*) mentions that the ovaries of *E. flabellatus* Fonsc. comprise only three folicles each and contain only a small number of developing eggs, indicating a capacity approximating that of the species above-mentioned.

The number of individuals which may develop to maturity upon a single host is often much greater than that indicated for the foregoing species. W. D. Pierce records 118 *E. zehntneri* Ferr. from a single caterpillar of (*Scirpophaga*) *Topeutes intacta* Sn.; Cherian and Israel (1937) reared a maximum of 170 of the same species from a caterpillar of the same genus in India, and the average for a series of host individuals was 75.

Information regarding the sex ratio in the family reveals that there is often a marked variation correlated with host size. In *E. hispidarum*, the males predominate in the ratio of 7 to 5 when development is solitary upon small hosts, whereas they are in the minority by 1 to 2 when several individuals develop upon each mature host larva. The ratio is decidedly variable among different colonies, but each always contains at least one male. A. W. Lopez observed a ratio of 8 to 1, the females predominating, in *E. zehntneri* in the Philippine Islands, whereas Pierce, in rearings of more than two thousand of the same species, found that only 8 per cent were females. In the few species in which parthenogenetic reproduction has been noted, the progeny have been males.

IMMATURE STAGES

The eggs of the Elasmidae are of simple form, either subcylindrical or kidney-shaped in outline, the anterior end slightly the wider and both ends smoothly rounded. That of *E. claripennis* Cam. is stated to have a short peduncle at the narrower end, and in *E. nudus* Nees (Parker, 1924) the chorion is covered with minute tubercles.

The first-instar larva is hymenopteriform, with the segmentation distinct and the body widest in the anterior abdominal region. That of *E. hispidarum* has a median row of fleshy pseudopodia ventrally, these being situated intersegmentally, the first between the second and third thoracic segments. In *E. nudus* (Fig. 52), the body is somewhat cylindrical and, like *E. hispidarum*, has spiracles on the second thoracic and the first three abdominal segments.

The second-instar larva of *E. hispidarum* is similar to the first, as is also the third, except for the appearance of the nine pairs of spiracles, situated on the second and third thoracic and the first seven abdominal segments.

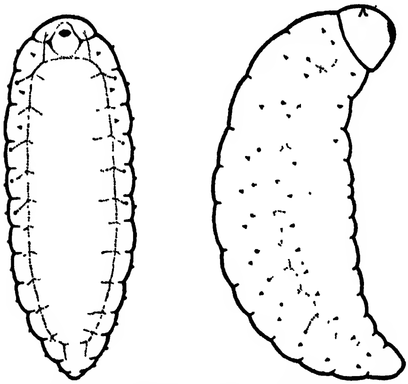


FIG. 52.—The first instar (left) and mature larvae of *Elasmus nudus* Nees. (*From Parker*, 1924.)

The mature larva, which is the fourth instar in *E. hispidarum*, bears a row of retractile intersegmental pseudopodia on the median line, both dorsally and ventrally. They are extruded only when the body is fully extended and presumably serve in locomotion within the host leaf mine. The spiracle number and arrangement in this species and in *E. nudus* (Fig. 52), also, are identical with those given above for the third instar.

The pupae of *E. hispidarum* and of an undetermined species reared from bagworms in Japan are distinguished by the extension of the scutellum into a distinct bifurcate process which, in the latter species, extends over about one-third of the length of the abdomen.

PTEROMALIDAE

The family Pteromalidae is one of the most common of the Chalcidoidea and includes many genera and species that are frequently encountered as parasites or hyperparasites of various major insect pests. The dominant genera include *Pteromalus*, *Habrocytus*, *Dibrachys*, and *Pachyneuron*. The majority of species are external gregarious parasites of lepidopterous and coleopterous larvae and pupae, but a number attack dipterous pupae and hymenopterous larvae. Several genera, such as *Enargopelte*, *Peridesmia*, and *Spintherus*, are egg predators. The occurrence of both external and internal parasitism within a genus is demonstrated in *Dibrachys*, *Pteromalus*, and *Stenomalus*. *Ophelosia crawfordi* Riley is remarkable in its adaptations in that it occurs as a predator upon the eggs of *Icerya*, *Pulvinaria*, and *Pseudococcus* (Smith and Compere, 1931) and as a hyperparasite of these genera and occasionally of coccinellid larvae, also. It has been reared in some numbers from adult *Icerya* females, in which it was possibly hyperparasitic, through *Cryptochaetum*. Several species of the genus *Asaphes* are known as hyperparasites of Aphididae through the various braconid, aphelinid, and encyrtid primaries (Griswold, 1929). The wide range of hosts that may be attacked by a single species is strikingly shown by *Dibrachys cavus* Wlk. (*boucheanus* Ratz.), for which 45 host species, comprising 2 Coleoptera, 2 Diptera, 27 Hymenoptera, and 14 Lepidoptera, are given by Faure and Zolstorewsky (1925).

The only species of the family that has proved to be of particular value in biological control is *Pteromalus puparum* L., which is a gregarious

internal parasite of the pupae of the cabbage butterfly, *Ascia rapae* L. In New Zealand it is credited with bringing about a marked reduction in the host population.

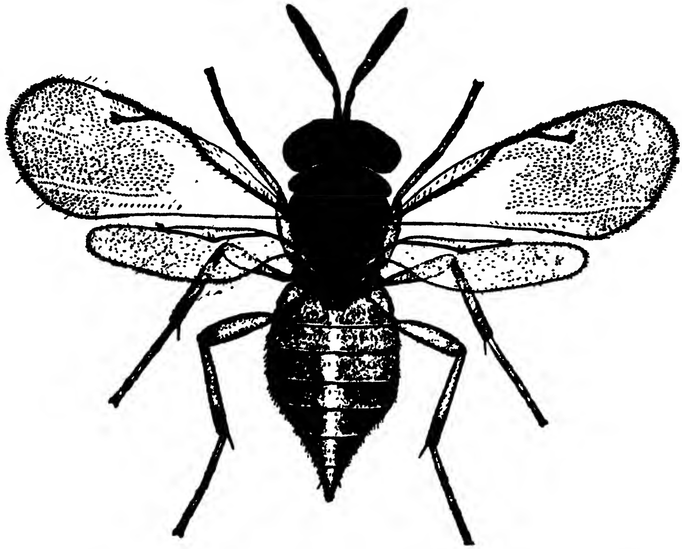


FIG. 53.—The adult female of *Habrocytus cerealellae* Ashm. (*From Noble*, 1932.)

BIOLOGY AND HABITS

The Pteromalidae present several features in their host relationships, life histories, and habits that are of particular interest, and a sufficient number of species have been studied in detail to give a basis for comparison. The most extended studies have been upon representatives of the genera *Pteromalus, Eupteromalus, Habrocytus, Mormoniella, Dibrachys*, and *Dibrachoides*.

Habits of the Adult.—The time intervening between emergence of the adults and the beginning of oviposition is comparatively short. Females of *Mormoniella vitripennis* Wlk. (*Nasonia brevicornis* Ashm.) have been observed to deposit eggs within three hours after emergence, and *Habrocytus cerealellae* Ashm. does so readily on the following day. A two to three days' gestation period is required by *Dibrachoides dynastes* Foerst. and *Homoporus braconidis* Ferr., but *Pirene graminea* Hal. deposits its first eggs seven or eight days after adult emergence.

The adults of this family, as well as those of most other families of the order, feed extensively upon honeydew, plant secretions, etc. These materials are sufficient to maintain life, but in a great many species they do not suffice to meet the nutritional requirements of the females for egg production. It has been demonstrated that a protein diet is

essential, at least in some species, before normal oögenesis can take place. The body fluids of the host insects provide a suitable food of this type, and the females of this family, more generally than of any other, have developed the habit of feeding upon the fluids that exude from punctures made with the ovipositor. This feeding may be associated with and immediately precede oviposition, or the two acts may be entirely independent and upon different host individuals.

Feeding upon exposed hosts presents no difficulties for the female parasite. But where they are contained in a cell, burrow, cocoon, or puparium, direct feeding is impossible, and, as a result, it is necessary to provide some means by which the body fluids of the host can be brought within reach of the mouth of the parasite. This is accomplished by the construction of a "feeding tube" which extends from the puncture in the host body to the outside of the wall of the cell or other space that it occupies. The fluids rise to the top of the tube by capillary action and are there lapped up by the parasite. In some species, the withdrawal of the body fluid is so great as to indicate the use of suction to bring it to the surface.

The discovery of this adaptation for feeding was made by Lichtenstein (1921) in the course of his studies upon *Habrocytus cionicida* Licht., an external parasite of the larvae and pupae of the weevil, *Cionus thapsi* F., in their cocoons. The habit has since been found in many other genera of the family and in occasional species of a number of other families of the Chalcidoidea. Its occurrence is known also among the Braconidae, most commonly in the genus *Microbracon*.

Fulton (1933) has given perhaps the fullest account of the manner of tube formation in *Habrocytus cerealellae*, which is a parasite of the angoumois grain moth, *Sitotroga cerealella* Oliv., in North America. It normally attacks the larval stage in its cell in the seed, though parasitization and development are possible upon exposed larvae. A feeding tube is constructed only when the host is so deeply embedded in the seed that it is out of reach by direct contact. After stinging is complete, the ovipositor is withdrawn until only its tip penetrates through the hole in the cell wall. A clear, viscid fluid begins to ooze from it, most copiously from near the tip. This material is spread by a twisting and vertical movement of the ovipositor, which serves as a spatula; it is worked downward gradually, and fresh material is added continuously until the body of the host is finally reached. The ovipositor tip is then slowly moved about until the original puncture in the skin is found. It is then reinserted in the puncture and held in that position for several minutes, and during this time the tube is completed. The withdrawal of the ovipositor is accomplished very slowly, in order not to damage the delicate tube; meanwhile, the stylets move alternately up and down.

A small extension of the tube appears above the surface of the opening in the cell wall. The female then turns about and begins feeding upon the fluids from the tube (Fig. 54); this may continue without interruption for a period as long as one hour. At the completion of feeding, she reinserts the ovipositor in the tube, apparently for the sole purpose of breaking it. Other authors have noted this reinsertion of the ovipositor by different species and consider it to be for the purpose of inducing a renewal of flow of the body fluids and that the breaking of the tube is only accidental.

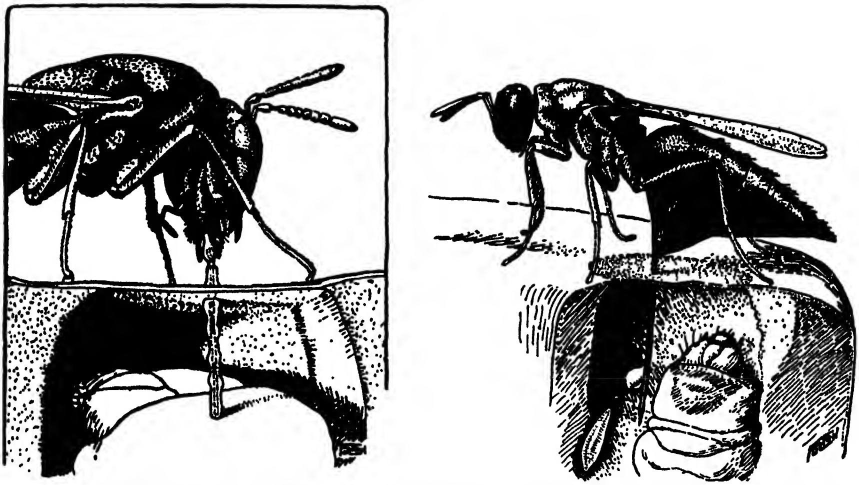


FIG. 54.—A female of *Habrocytus cerealellae* Ashm. in the act of oviposition and, at left, feeding from the tube which she has constructed. (*From Fulton*, 1933.)

An identical manner of tube formation has been described by Faure and Zolstorewsky in the case of *Dibrachys cavus*, but this is not uniform for all species. H. D. Smith (1930) observed that in *Dibrachoides dynastes* Foerst. the chalky-white fluid flows down the full length of the ovipositor while its tip is still inserted in the wound. Hardening takes place quickly, and the ovipositor is slowly and cautiously withdrawn.

Attention has been called by Flanders (1935*b*) to the construction of the feeding tube by species that are egg predators. The female of *Spintherus* sp. punctures one of a cluster of eggs of the alfalfa weevil, *Hypera variabilis* Hbst., that are embedded in the plant stem, forms a feeding tube, and sucks out the entire contents. The material from which the tube is made is apparently produced by the colleterial glands.

In certain species, feeding is not limited to the host fluids but is upon the tissues as well. Noble (1932) found that when the ovipositor of *Habrocytus cerealellae* is withdrawn from the wound the barbs of the sheath draw up strands of solid matter and the parasite then chews vigor-

ously upon them. Graham (1918) records the same habit in *Dibrachys clisiocampae* Fitch, which attacks the mature larva of the bee moth in its cocoon.

Flanders has also made a detailed study of the relation of the feeding habit of *Peridesmia* and *Spintherus* to egg development. Sufficient protein is not stored up during the larval period to provide for egg production, and this deficiency must be made up later. The preference for host fluids is exhibited only during oögenesis and maturation. This reaction first appears about six days before egg deposition. If environmental conditions are adverse for oviposition, the ovarian folicles are absorbed, feeding on host fluids ceases, and a long period of inactivity, so far as reproduction is concerned, ensues. The degeneration of the ovaries under these conditions is considered to be a form of phasic castration. This induced inactivity corresponds in time to periods of low numerical status of the stage of the host insect that is subject to attack. It may have a direct bearing upon the ability of a parasite species to survive where the host itself has the habit of undergoing a long period of estivation.

Restriction of feeding to protein substances enables the female to develop and deposit eggs for a certain period, but carbohydrates are essential to provide the energy required for extended activity. Doten (1911) mentions that females of *Pteromalus puparum* deposited eggs for a period of three weeks when confined with fresh host pupae, to which they were limited for food, whereas with the addition of honey they continued oviposition for two months.

Roubaud (1917) was apparently the first to realize the significance of this host-feeding habit. Working with *Mormoniella vitripennis*, he determined that such feeding was essential before normal oviposition could take place.

In the great majority of species that attack lepidopterous and coleopterous larvae, the host is permanently paralyzed prior to oviposition. This appears to be especially true of *Habrocytus*, *Dibrachoides*, *Dibrachys*, and several less common genera. In *H. cerealellae*, the parasite pumps several droplets of a paralyzing fluid into the host body, which can be readily seen as it flows down the ovipositor. This organ is thrust deeply into the host to ensure thorough distribution of the fluid. The act of stinging requires up to 10 minutes, and the host is completely paralyzed before the ovipositor is withdrawn. In *Dibrachoides dynastes* the host is said to be stung 3 to 100 times before complete immobility is secured, and this may require up to eight hours. The larvae of the bee moth, *Galleria mellonella* L., die from the effects of the sting of *Dibrachys clisiocampae*, and the eggs of the latter are not deposited until death has taken place. Doten states that larvae of the codling moth

and pupae of the cabbage butterfly are usually killed by the ovipositor thrusts of *Meraporus* sp. In a very considerable number of species, the hosts are consistently killed by the sting, and decay sets in very soon thereafter. In these cases, the larvae are really scavengerous in habit, rather than parasitic. A few species do not paralyze the host; among these is *Trichomalus fasciatus* Thoms., which is an external parasite of the larva of *Ceutorrhynchus assimilis* Payk. *Pirene graminea* paralyzes its host larva *Contarinia pisi* Winn. only temporarily.

Several authors have called attention to the habit in various species of the family, parasitic in dipterous pupae, of sealing the puncture in the puparial wall with a drop of fluid after the completion of oviposition.

Scymnophagus townsendi Ashm. is an external parasite of the pupae of *Scymnus* sp., a coccinellid predator on aphids in Japan. In oviposition, the female stands upon the exposed portion of the dorsum of the pupa and makes a preliminary insertion of the ovipositor to form a feeding puncture. Several hours may be spent in lapping up the body fluids exuding from the wound; after this is complete, the ovipositor is reinserted, usually in the original puncture, and forced completely through the body. The egg is deposited on the ventral surface of the abdomen or under a wing pad or leg. Feeding and oviposition may be repeated, the single original puncture being utilized, and a compact cluster of four to six eggs is usually found when the host is finally abandoned.

The mechanics of oviposition in *H. cerealellae*, as described by Fulton, reveal a remarkable adaptation for the passage of a large object through a relatively minute tube such as the ovipositor. The small end of the egg approaches the ovipositor first; the spicules of the chorion, in conjunction with the backward-directed spines and ridges on the walls of the vagina and stylets, prevent any backward movement once the surfaces are engaged. The tip of the egg is greatly compressed and is drawn down through the ovipositor. The chorion is capable of considerable stretching, and passage down the ovipositor is by a pulling action rather than the result of pressure exerted through the abdomen. Thus the portion of the chorion being drawn through the tube is almost devoid of liquid content, and consequently little lateral pressure is exerted on the ovipositor. During this time, the stylets, moving together rather than alternately, work the tip of the egg downward until it reaches the end of the ovipositor (Fig. 54). As soon as this is accomplished, the egg contents flow down the tube into the released portion, and by this action the remainder of the egg is pulled through the ovipositor. The reduction in diameter of the egg during its passage down the ovipositor is shown by a comparison of egg size with ovipositor width. The egg averages 0.16 mm. in width, whereas the outside diameter of the ovipositor is approximately one-fifth of this, or 0.03 mm.

The swarming habit of adults, which is of rare occurrence in Chalcidoidea, is recorded for *Pteromalus deplanatus* Nees (Scott, 1919). From 1916 to 1919 in certain localities in England, they were present in enormous swarms in buildings during late July and August. This is probably not a true swarming but merely attraction of large numbers to a common environment, possibly in the search for suitable quarters in which to pass the winter.

The reproductive capacity of many species of Pteromalidae is relatively high. An egg deposition of 676 in 78 days has been recorded by Fulton for *H. cerealellae*, and *P. puparum* has been found to deposit up to 697 eggs. A single female of *Mormoniella vitripennis* produced 557 progeny (Cousin, 1933), indicating an egg capacity appreciably in excess of that number. A series of *Eupteromalus nidulans* Thoms. females deposited an average of 251 eggs, with a maximum of 583 (Proper, 1931). *Aplastomorpha calandrae* How. deposits approximately 250 and *Dibrachoides dynastes* a maximum of 122 during a period of one month.

Larval Development.—The first-instar larvae of the external feeding species are usually quite active and move about readily on the body of the host and in the cell containing it. Smith states, however, that larvae of *D. dynastes* which hatch from eggs not placed directly upon the host usually die without reaching it. In the solitary species, there is a very pronounced cannibalistic tendency, and the larva that hatches first will often destroy the remaining eggs. In case a number are able to hatch, the youngest is usually victorious in the combat for possession of the host, owing to its greater mobility. This mode of elimination of the surplus individuals seems necessary in view of the indiscriminate oviposition by the parent female. She is apparently unable to recognize host individuals already parasitized or at least does not refrain from again depositing eggs upon them.

In *Pteromalus puparum*, many individuals of which develop within a single host pupa, it often happens that the colony is too large for the available food supply. Hardy (1933) states that numerous dead larvae are often found at the extremities of the pupa, these having died from starvation. It is quite evident that the food material at these points is exhausted more quickly than at the middle of the body. Faure (1926) states that development of individuals in the extremities of the host is retarded, but Voukassovitch (1926) concludes that the retardation in emergence of a portion of the brood is independent of the nutrition factor. He found that emergence from pupae that had been parasitized on known dates often extended over several months. This appears to be a larval diapause of uncertain duration and affects a varying portion of each colony. It is decidedly unusual, however, for the individuals comprising a single colony of an internal parasite to emerge so irregularly.

This contrasts sharply with the synchronous development and emergence of the polyembryonic Encyrtidae, which encounter the same adverse conditions through overcrowding, etc.

Certain of the solitary ectophagous species show a considerable adaptability as regards the size of host individuals upon which development can be completed successfully. Noble found that *Habrocytus cerealellae*, when developing upon small *Sitotroga* larvae, is able to pass through the final larval stage without feeding and to attain the adult stage. In these instances, the larval stage is prolonged, and the resulting adults are of minute size.

The fourth-instar larva of *Stenomalus micans* Ol., parasitic in the larva of *Chlorops taeniopus* Meig. (Kearns, 1931), is equipped with a specialized boring apparatus upon the head that is employed to break up the internal organs of the host and to effect emergence through the hardened shell of the host larva, which has died just as it was undergoing the first phases of pupation. The fifth larval stage represents a non-feeding period, which is of short duration.

Parasitism by *Stenomalus* results not only in changes in the appearance of the host larva but in its activities as well. Healthy larvae move downward in the barley stem and, just before pupation, turn about and ascend to a point immediately below where the leaf leaves the stem; at this point, the reddish-brown puparia are formed. Parasitized individuals do not make this reversal in position, and the partly formed puparia remain colorless.

There are several departures from the normal pupation habit of the family. This transformation usually takes place in the cell, cocoon, or other cavity in which the host was contained. *Eupteromalus nidulans* forms a naked pupa in the web of its lepidopterous host. The pupa of *Mormoniella vitripennis* retains the larval exuviae about the posterior portion of the abdomen, and this, adhering to the meconium, attaches the pupa to the wall of the host puparium.

Enargopelte ovivora Ishii is one of the few Chalcidoidea that show a tendency toward normal cocoon formation (Ishii, 1928). The mature larvae, of which there may be about 10 in the egg chamber of *Lecanium* sp., spin individual, yellowish-brown cocoons.

The number of individuals which develop upon or in a single host is very large in some species. Martelli (1907) records 165 adults of *Pteromalus puparum* from a single pupa of the cabbage butterfly, and Picard (1922) reared 212 males from the same host and as many as 47 *Tritneptis klugii* Ratz. (*P. nematicidus* Pack.) have been secured from a cocoon of *Lygaeonematus erichsonii* Htg. (Hewett, 1912). Roubaud reared 105 *M. vitripennis* from a single dipterous puparium. These figures probably represent the maximum for which food material was

available. In most gregarious species, however, development to maturity is possible even if only a portion of the available food material is utilized. The various species of *Dibrachys* usually develop in numbers of less than 10 on each host, and all the recorded species of *Habrocytus* are solitary.

Life Cycle.—The life cycles of the pteromalid species are usually quite short, averaging approximately three weeks from egg to adult, with a minimum of 10 days recorded for *Habrocytus cerealellae* and *M. vitripennis*. The females of many species require 1 or 2 days longer for development than do the males. The incubation of the egg requires from less than 1 day to 3 days, the larval stage 4 to 10 days, and the pupal stage 4 to 14 days. A conspicuous exception is *E. ovivora*, in which the egg, larval, and pupal stages require 7 days, 20 days, and approximately 11 months, respectively.

The number of generations per year is largely dependent on availability of suitable host stages, and most species produce generation after generation as long as these are available. Some species are strictly limited to a fixed number. *E. ovivora* has only one each year, corresponding to the cycle of the host. *Pirene graminea* and *Stenomalus micans* have two generations, as do their respective hosts. *Aplastomorpha calandrae* (Cotton, 1923) and *H. cerealellae*, on the other hand, are able to produce several generations to each one of the host. In these two species, there is no need for synchronization of the cycles of parasite and host, for they attack insects infesting stored grains, which are present in all stages throughout the year. *Tritneptis klugii* has about six generations each year upon one brood of its host.

Hibernation of the majority of species takes place in the mature larval stage within the host cell, cocoon, or puparium. *Eupteromalus nidulans*, however, is found in the hibernation webs of the satin and brown-tail moths. *E. ovivora*, *Merisus febriculosus* Gir., and *Rhopalicus suspensus* Ratz. pass the winter in the pupal stage, whereas *Dibrachoides dynastes* and *Pseudocatolaccus asphondyliae* Masi persist through the winter in the adult form. Several others may pass the winter as either mature larvae or adults.

A number of species are capable of undergoing protracted periods of inactivity in either the larval or the adult stage when conditions are unfavorable for development. The relation of food to reproduction in *Spintherus* and *Peridesmia* has already been discussed, and it was shown that phasic castration in the females may continue for a long period. This is one means of maintaining a species during periods of adverse conditions; another is a larval diapause, such as occurs in *H. medicaginis* Gahan and *Mormoniella vitripennis*. In the former species, individuals have been noted to pass nearly two years in the larval stage, as con-

trasted with the normal two weeks. *M. vitripennis* in dipterous puparia may also, under certain conditions, persist for several years.

The length of adult life is considerably greater than in many other families of the Chalcidoidea. Those species which normally pass the winter in the adult stage are, of necessity, exceptionally hardy, and *D. dynastes,* which is representative of this group, has been kept alive for eight months or more at temperatures of 5 to 13°C. Species that do not have this hibernation habit usually live six to eight weeks.

Sex Ratio and Parthenogenesis.—The known sex ratios of species of the family indicate a varying preponderance of females ranging up to 30 to 1 in *Habrocytus medicaginis.* Various authors have given figures for *M. vitripennis* which range from 1:1 to 10:1. The normal ratio for *P. puparum* is approximately 2 to 1; yet George (1927) calls attention to a seasonal variation, the ratio being 2.8 to 1 in the spring generation and 1.1 to 1 in that developing in the autumn. In *H. cerealellae,* the field ratio is approximately 3 to 2. It has been determined experimentally that the proportion of male progeny increases toward the end of the life of the females. Griswold records an excess of males in the ratio of approximately 3 to 1 in limited rearings of *Asaphes americana* from aphids collected in greenhouses.

IMMATURE STAGES

The eggs of the great majority of the species of the family are ovate, ellipsoidal, or cylindrical in form, often slightly curved, and without an anterior stalk or pedicel of any sort. That of *Enargopelte ovivora,* however, is an exception in that it has a slender stalk, one-third as long as the egg body, at the broader end. In many species, the chorion is smooth and shining; in others, it is covered with minute spines or spicules, but with the poles bare (Fig. 55*A*). These spicules often give the egg a grayish color. The eggs of *Dibrachys cavus, Stenomalus muscarum,* and *Habrocytus trypetae* Thoms. are covered with "tubercles," or papillae; those of *Pachyneuron coccorum* L. have a granulate surface. In *Dibrachoides dynastes,* the chorion bears longitudinal ridges. The sculpturing of the egg is not uniform even within a genus, as shown by the smooth glistening egg of *Pteromalus puparum* and the spinose chorion of that of *P. variabilis* Ratz. The sculptured chorion is found only upon eggs that are deposited externally.

The first-instar larvae of practically all species are hymenopteriform, with 13 distinct body segments, the head often large, and the integument bare except for three pairs of setae on each of the thoracic segments and two pairs on those of the abdomen; the four pairs of spiracles are situated on the second thoracic and the first three abdominal segments (Fig. 55*B*). There appears to be a variation among the species in the number of sensory setae. The body of *Stenomalus micans* is covered with minute integumentary setae, and the last abdominal segment is modified to form a "furca" which serves to hold the larva in a favored feeding position. *Habrocytus* sp. reared from braconid cocoons by Voukassovitch (1927) has a sucker-like organ ventrally on the second thoracic segment, which is stated to serve a locomotory function. *Merisoporus chalcidiphagus* W. & R. has an additional pair of spiracles, which is on the third thoracic segment. Certain of the endophagous species, such as *Pteromalus puparum,* lack an open tracheal system.

The larva of *Pirene graminea*, described and figured by Kutter (1934), departs from the normal of the family and is distinctly mandibulate in form. The head is large, the body segmentation indistinct, the integument without setae, and the large, extruded, falcate mandibles are very widely spaced and lie transversely. Marchal (1907) describes a larva of similar form in *Tridymus piricola* Marchal.

The full complement of five larval instars has been described for *Eupteromalus nidulans*, *E. fulvipes* Forbes, *Dibrachoides dynastes*, *Pachycrepoideus dubius* Ashm., *S. micans*, and *Merisus destructor* Say. *Dibrachys cavus* and *H. cerealellae*, both of which have been studied in detail, apparently have only four, and *Habrocytus* sp. discussed by Dustan has only three. Kutter describes only two for *Pirene graminea*, though his prepupa shows distinctive characters representing presumably a third instar.

The second-instar larvae of all species are of simple form, with the sensory and integumentary setae reduced in size; the latter are often absent. The nine pairs of spiracles occur on the last two thoracic and the first seven abdominal segments. In *H. cerealellae*, only the four pairs that persist from the first instar are open immediately

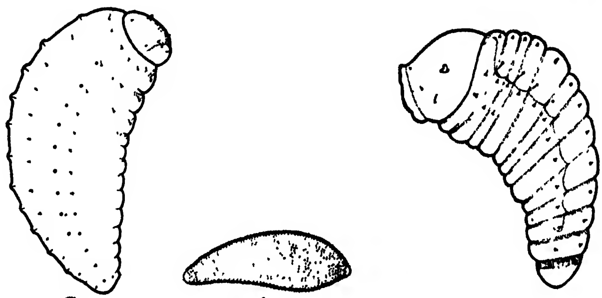


FIG. 55.—Immature stages of the Pteromalidae. *A*, the egg of *Habrocytus cerealellae* Ashm. (*from Noble*, 1932); *B* and *C*, first-instar and mature larvae of *Pseudocatolaccus asphondyliae* Masi. (*from Parker*, 1924).

after the molt, and the additional five, which are smaller, appear later in the stage. The larva of *P. graminea* is indistinctly segmented, and the head is much reduced, with the mandibles small, curved, and very widely spaced.

The fourth-instar larva of *S. micans* is distinguished from other larvae of the family by a heavily sclerotized boring armature on the head. This consists of a transverse plate with a serrate edge situated immediately above the labrum and one or two heavy conical spines on the median line below the antennae.

The mature larvae of the different species are uniform in their characters and present no general distinguishing features. The mandibles are simple, and the integument is smooth, with the sensory setae reduced in size. In *H. cerealellae*, there are three pairs of prominent spines at the end of the last abdominal segment. This species and *Pseudocatolaccus asphondyliae*, show pronounced intersegmental ridges dorsally. The tracheal system usually has nine pairs of spiracles, situated as on the second instar. However, Haviland (1922*b*) records 10 pairs for *Asaphes vulgaris* Wlk.; the first of these is situated on the intersegmental membrane between the first and second thoracic segments, and those following are on the third thoracic and the first eight abdominal segments. There is a vestigial tenth pair on the eighth abdominal segment in *H. trypetae* Thoms. The spiracles of *S. micans* first appear on the fourth instar, and rudimentary spiracular stalks are also present on the first thoracic and the eighth abdominal segments. Kutter's figure of the prepupa of *Pirene graminea*, which bears the external structures of the mature larva, shows the last segment produced into tube-

like form and bearing two pairs of strong setae at the distal end. This tube is stated to be retractile.

Kearns describes an unusual development of the internal tracheal system in the endophagous first- and second-instar larvae of *S. micans* (Fig. 56). Both instars possess the usual longitudinal trunks, with dorsal and ventral commissures at the anterior and posterior ends, respectively, and blind spiracular stalks in the last two thoracic and the first eight abdominal segments. In addition, a pair of visceral tracheal trunks arise from the anterior commissure and extend over the dorsum of the intestine to the eighth abdominal segment, where they unite. These visceral trunks were not detected in the third- to fifth-instar larvae. A comparable modification of the tracheal system is not known in any other hymenopterous larva.

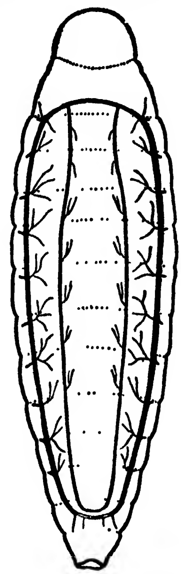


FIG. 56.—The tracheal system of the second-instar larva of *Stenomalus micans* Ol., showing the supplementary longitudinal visceral tracheal trunks extending from the anterior commissure along the dorsum to the eighth abdominal segment. (*Redrawn, after Kearns*, 1931.)

Another departure from the normal respiratory system is described by Dustan (1923) for the larva of *Habrocytus* sp. parasitic in *Rogas* pupae. His description of that of the mature larva is as follows: "Perhaps the most amazing thing about this parasite is its immense tracheal system which, as was said previously, almost fills the body cavity. It has a tracheal trunk running down each side of the body and spiracles that can be made out under the 4 mm. objective, which appear to be closed, however; but more unusual than all, it possesses myriads of tracheids packed into every conceivable part of the body. These tracheids are collected into bundles or areas which are held in place by a definite wall or membrane. Just inside the wall of each bundle we find a ring of tracheids, varying somewhat in size but alike in having extremely thin walls. All the space inside the tracheids is packed with blood corpuscles and plasma, so that each bundle really consists of a tracheal sheath, the inside of which instead of being hollow is filled full of blood. . . . These tracheids open at the hypodermal wall and in this way secure an abundant supply of oxygen from the blood stream of the host. This oxygen is then carried in the tracheal bundles to all parts of the parasite and distributed by the blood stream to the different organs and tissues."

SPALANGIIDAE

The family Spalangiidae comprises a small number of genera, of which *Spalangia* is the one most commonly encountered. In a review of the host preferences of this genus, Richardson (1913) lists six species from dipterous hosts, one from Lepidoptera, and two with myrmecophilous habits. The recording of one on a lepidopterous host is probably an error, for the species concerned, *S. nigra* Latr., has since been recorded from housefly puparia. Silvestri (1914) records several species from the puparia of Trypetidae in West Africa. Those which attack Diptera confine themselves to the puparia and are solitary and external in habit. They are essentially parasites of dipterous pupae and consequently are considered hyperparasites only when the particular host species that they

attack are themselves of parasitic habit, though *S. drosophilae* Ashm., which attacks dung-infesting Diptera, is recorded as attacking *Alysia* and *Psilodora*, which are primary parasites of the same hosts. Entomophagous Diptera which form their puparia on or near the soil surface are frequently attacked by members of this genus. *Cerocephala* develops upon larvae and pupae of the coleopterous families Scolytidae, Curculionidae, etc.

The principal value of the Spalangiidae in the natural control of insect pests is in the reduction of various Diptera found in decaying flesh, dung, and other refuse. Lindquist (1936) records up to 64 per cent

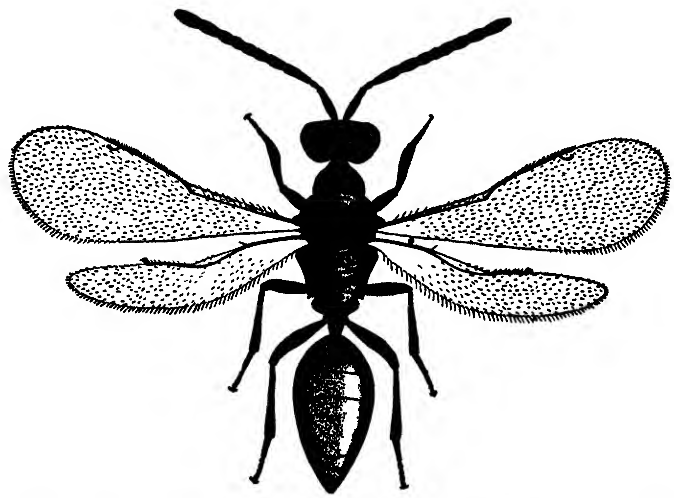


FIG. 57.—The adult female of *Spalangia* sp. (*From Clausen, et al.*, 1928.)

parasitization of dung-infesting Diptera, mainly by *S. muscidarum* var. *stomoxysiae* Gir. Attempts have been made to utilize several members of the family in the biological control of the horn fly and fruit fly in Hawaii and the horn fly in Australia. In none of these instances, however, has the species introduced exerted any appreciable check upon the host.

BIOLOGY AND HABITS

The most extensive study of a representative of the Spalangiidae is that by Richardson on *S. muscidarum* as a solitary parasite of the pupae of the housefly, *Musca domestica* L. Other species of the genus having dipterous hosts will probably be found to possess similar habits.

In oviposition, the female crawls over the host puparium, examines it carefully with the antennae, and then inserts the ovipositor through the puparial wall, usually in the posterior half. The body of the larva or

pupa within the puparium is not penetrated, and the egg is placed externally.

The first-instar larva is very active and is capable of extended movement over the surface of the body of the host. This is apparently for the purpose of finding a suitable point for feeding, which usually proves to be the dorsum or dorsolateral areas of the abdomen. The skin of the pupa is much thinner at these points and is more easily punctured than elsewhere. The second- and third-instar larvae have a fixed feeding position. After the completion of feeding, the mature larva moves toward the anterior end of the puparium, casts its meconium, and then transforms to the pupal stage. The adult emerges through a hole cut in the anterior end of the puparium.

Pinkus (1913) has published an account of this species as a parasite of the stablefly, *Stomoxys calcitrans* L., which differs in several respects from that given by Richardson. Oviposition is said to take place in the anterior portion of the puparium, usually through a suture. The female is able to detect prior parasitization and will not deposit a second egg upon a host already bearing one. Many of the pupae attacked die, even though no egg is deposited, which would indicate that the body had been penetrated by the ovipositor. The adults mate very soon after emergence, and the females are able to deposit eggs the same day.

The minimum life cycle under laboratory conditions was found to be about 88 days. Under summer conditions, the cycle is probably less than half as long as that given. Hibernation apparently takes place in any immature stage, and development progresses at any time that the temperature becomes sufficiently high.

Handschen (1932, '34) has recently studied two species of *Spalangia* that parasitize the pupae of *Lyperosia*, one being *S. sundaica* Graham of Java and the other *S. orientalis* Graham, native to Australia. *S. sundaica* was found to deposit an average of 160 to 170 eggs during a period of about four weeks. The cycle from egg to adult is completed in 18 to 21 days, and the males emerge 2 days earlier than the females. The adult wasps are greatly attracted to dung, in which the hosts develop. *S. orientalis* has the same general habits and life cycle as the above species but produces an average of only 85 eggs, during a 15-day period. These two forms were crossed in an effort to produce a more effective race and one better adapted to Australian conditions. The female *S. orientalis*, when mated with male *S. sundaica*, produced progeny more prolific than either parent form, the average egg deposition being 240 in a 32-day period. The reverse cross gave an egg deposition of only 100 during a 10-day period.

Cerocephala cornigera Westw. (Russo, 1926, '38), which is parasitic upon scolytid larvae and pupae, first paralyzes the host and then places

the egg either directly upon it or in its immediate vicinity. The female usually inserts the ovipositor into the entrance of the oviposition tunnel of the host.

The feeding habits of the adults of the family are very incompletely known. Lindquist (1936) states that *Spalangia muscidarum* var. *stomoxysiae* pays very little attention to artificial foods, and the length of life when confined with puparia indicates host feeding. Parker and Thompson (1925) state that such feeding occurs in *S. nigra* Latr., and a feeding tube is constructed.

The life cycles of members of the family are uniformly short, ranging from a minimum of 17 days in *S. muscidarum* var. *stomoxysiae* and *S. drosophilae* to 25 to 30 days in *C. cornigera*. Several generations are produced each year, and the winter is normally passed in the mature larval stage, though Richardson states that *S. muscidarum* is in the pupal stage during that period.

The sex ratio has not been determined with exactness for any species, though the females are reported to predominate in the ratio of 2 to 1 in *S. muscidarum* var. *stomoxysiae*. Parthenogenetic reproduction has been observed in several species of *Spalangia*, the progeny in each case being male only.

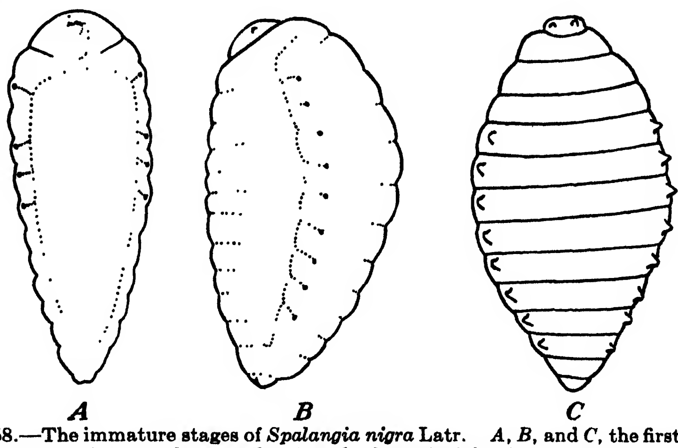


FIG. 58.—The immature stages of *Spalangia nigra* Latr. *A*, *B*, and *C*, the first-, second-, and fourth-instar larvae, the last showing the lateral abdominal tubercles characteristic of the genus. (*From Parker*, 1924.)

IMMATURE STAGES

The eggs of *S. muscidarum* and *S. nigra* are elongate-ovate in outline and broader at the anterior end, which bears a nipple-like protuberance. That of *Cerocephala* is of similar form except that the anterior protuberance is lacking.

The first-instar larvae are hymenopteriform and elongate-oval in outline and have a relatively large head. In *S. nigra* (Parker, 1924), each body segment bears a band of minute setae at the anterior margin. An open tracheal system is found in *S. nigra*

with the spiracles occurring on the second thoracic segment, or on the membrane between the first and second, and on the first three abdominal segments (Fig. 58 *A*). Richardson emphasizes that not only does the first-instar larva of *S. muscidarum* lack spiracles but the intermediate and mature larvae are likewise apneustic.

The number of larval instars in the family is uncertain, with only three mentioned for *S. muscidarum* and four for *S. nigra.* The second- (Fig. 58*B*) and third-instar larvae of the latter species bear nine pairs of spiracles, situated on the second and third thoracic and the first seven abdominal segments.

The mature larvae of the genus *Spalangia* (Fig. 58*C*) are distinguished by the possession of distinct conical protuberances or tubercles at each dorsolateral margin of the first eight abdominal segments. A minute pair is found on the first thoracic segment. These tubercles have not been noted upon larvae of other genera. They are considered by Richardson to have neither an ambulatory nor sensory function, but appear to relate to prepupal growth. The mature larva of *C. cornigera* is more elongate than that of *Spalangia,* and each body segment bears four pairs of setae, those of the last segment being longest.

EULOPHIDAE

This family is relatively large in number of genera and species, and many of them are frequently encountered as parasites of important crop pests. Because of the wide range in host preferences and diversity in habits, they will be discussed by subfamilies.

In spite of the general occurrence of Eulophidae as parasites of crop pests, very few species have been successfully utilized in biological control. An outstanding example, however, is *Pleurotropis parvulus* Ferr., parasitic upon the leaf-mining hispid beetle, *Promecotheca reichei* Baly, a serious pest of coconut. This species was imported into Fiji from Java in 1932 and is credited with bringing about complete commercial control. It has since been colonized in a number of South Pacific islands where coconut is seriously damaged by beetles of this genus.

The species of the subfamily Eulophinae are usually of small size and often of brilliant metallic coloring, and the males of many species possess branched antennae. They are found principally as external parasites of dipterous, lepidopterous, and hymenopterous leaf miners or of larvae of these orders which bore in stems. The most frequently encountered genera are *Eulophus,* parasitic upon stem-boring lepidopterous larvae, etc., *Sympiesis,* upon lepidopterous and dipterous leaf miners, *Microplectron,* in sawfly cocoons, and *Cratotechus,* upon free-living lepidopterous larvae. Cushman (1926) calls attention to the host preferences of *Sympiesis* sp., which attacks coleopterous, dipterous, and hymenopterous leaf miners and also develops as an external parasite of the eggs of *Cimbex,* and he concludes that the location rather than the type of host is the determining factor in selection.

Although the majority of species are obligate primary parasites, yet a few are known to develop in the role of hyperparasites. *Dimmockia incongruus* Ashm. and *D. pallipes* Mues. are gregarious secondary

parasites of the gypsy moth, through *Apanteles* and other Braconidae, Ichneumonidae, and, more rarely, Tachinidae (Muesebeck and Dohanian, 1927). *Cirrospilus* is often reared from lepidopterous cocoons, in which it develops as a secondary parasite, through the larvae and pupae of Braconidae and Ichneumonidae.

The subfamily Tetrastichinae is of cosmopolitan distribution, and its species are mainly primary parasites of the immature stages of a wide variety of insects. The dominant genus is *Tetrastichus*, of which a number of species are egg parasites or predators and others attack the larvae or pupae of Coleoptera, Lepidoptera, and Diptera. They occur less frequently as parasites of Chermidae and Cynipoidea and as predators upon leaf mites. Some of those attacking Lepidoptera may be both primary and secondary in habit, whereas others are strictly hyperparasites, through the Tachinidae and various Hymenoptera. The species of *Melittobia* exhibit a wide range in host preferences, and many of them develop indiscriminately as primary or secondary parasites of a large series of hosts. The genus *Thripoctenus*, so far as known, is limited to thrips.

Relatively little is known regarding the host preferences and relationships of the subfamily Entedontinae. The records available indicate that the species are principally internal parasites of the larvae of Diptera, Coleoptera, and Lepidoptera contained in cases and leaf mines and in cells in plant stems. The leaf-mining Diptera, particularly the Agromyzidae, are especially subject to attack. A considerable number of species develop as hyperparasites. The most frequently encountered genera are *Chrysocharis*, attacking lepidopterous and dipterous leaf miners, and *Pleurotropis*, which develops in the larvae of Lepidoptera, Coleoptera, Diptera, Hymenoptera (Cephidae), etc., in stems of plants and also as a hyperparasite of other members of this and related families. A few species are known to be parasitic in or predaceous upon the eggs of Coleoptera and Homoptera.

The subfamily Elachertinae is a relatively small group of which only a few species have been studied. They are usually external parasites of lepidopterous larvae, particularly of the Noctuidae, Geometridae, Tortricidae, etc. The genera most commonly encountered are *Elachertus* and *Euplectrus*, both of which are cosmopolitan in distribution. The several species of the latter genus that have been observed are distinguished by their ectoparasitic manner of development upon free-living hosts.

BIOLOGY AND HABITS

Eulophinae.—An extended account of *Eulophus viridulus* Thoms. a parasite of the European corn borer, *Pyrausta nubilalis* Hbn., has recently

been given by Parker and Smith (1933*a*). It is a gregarious external parasite of the last three larval instars, and the number that develop upon each host ranges from only 2 or 3 to a maximum of 57. The average of the summer-generation colonies was 7.6 as compared with 16.5 for the fall brood and 23.3 in the winter generation.

The females require a relatively long period of gestation, and at no time is there a large number of eggs in the ovaries. The host larva is permanently paralyzed by the sting of the parasite, and the eggs are then laid indiscriminately upon the body. The larvae develop very

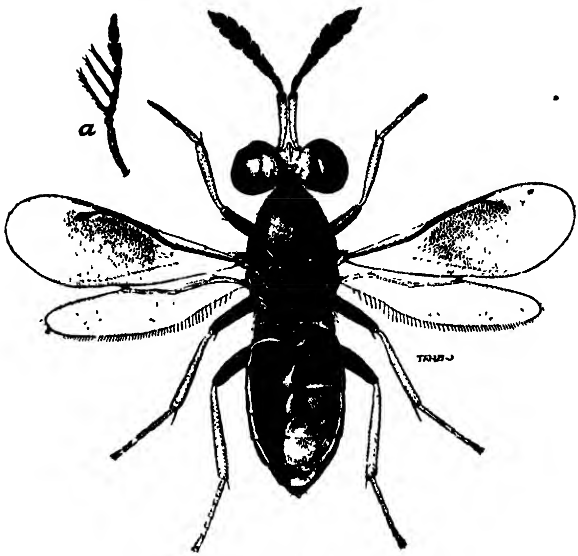


FIG. 59.—The adult female of *Microplectron fuscipennis* Zett., with (*a*) antenna of the male. (*From Morris and Cameron*, 1935.)

rapidly, and the host is reduced to an empty skin within a few days. When mature, the larvae crawl some distance away from the host and pupate in the host tunnel. The meconium is cast in the form of a series of blackish pellets, after which the final larval molt takes place. The cast skin still envelops the tip of the abdomen of the pupa and securely fastens it upon its dorsum to the wall of the tunnel. When the adult is ready to emerge, the pupal skin breaks transversely at the neck and longitudinally for a short distance along the median dorsal line of the thorax.

The winter is passed in the pupal stage in the host tunnel. Hibernation appears to be a true diapause, for it is not possible to secure early emergence by subjecting recently formed pupae to high temperatures. There are three generations each year, and the adults of the first brood

emerge in late April and May. The life cycle from egg to adult requires approximately 14 days under summer conditions.

Under field conditions, the females predominate in the ratio of about 2 to 1. Many colonies were found to consist of one sex only, particularly of females. Mating probably takes place in the host tunnel prior to emergence.

Microplectron fuscipennis Zett. (Fig. 59) is parasitic externally upon the mature larvae, prepupae, and pupae of the sawfly, *Diprion sertifer* Geoff. and others of the genus in Europe, and extended biological studies have been made upon it incident to its introduction and utilization in Canada in the attempt to control the spruce sawfly, *D. polytomum* Htg. (Morris and Cameron, 1935; Ullyett, 1936; Reeks, 1937).

Oviposition takes place in the sawfly cocoons in rubbish on the surface of the soil or slightly beneath it. The host is partly paralyzed, and 20 or more eggs are deposited upon the body, though a maximum of 120 individuals are able to attain maturity in a cocoon of *D. sertifer*. The average number varies greatly according to locality and ranged from 30.7 in Hungary to 72.5 in the collections made in Jugoslavia. The maximum number of eggs secured from a single female was 215, and the average number of progeny produced ranges between 40 and 57; consequently, it is seen that the number of cocoons that may be successfully attacked by a female is very small.

The cycle from egg to adult is completed in a minimum of about 20 days at a temperature of 22°C. Ullyett points out that, though high humidity is conducive to maximum oviposition efficiency, yet it has little influence upon larval development. This is explained by the existence within the cocoon of a microclimate which is largely independent of external conditions. The optimum developmental temperature is 20 to 35°C.

Hibernation takes place in the larval, prepupal, or pupal stages and, in so far as the great bulk of larvae and prepupae is concerned, appears to be a true diapause, for many enter this condition as early as August.

Morris and Cameron found that the sex ratio varied appreciably in different geographic sections. There is a great preponderance of females, ranging from 4 to 1 in Jugoslavia to 6 to 1 in Hungary, and the former ratio was secured also in a large series of laboratory-reared broods. The lower ratio in Jugoslavia may be correlated with the much higher number of individuals developing in each cocoon, as mentioned above. Reeks found that the ratio among progeny of females known to be mated was 9 to 1.

Several interesting points have been brought out by Taylor (1937) in his study of *Dimmockia javana* Ferr., a solitary external parasite of the larvae of the coconut leaf miner, *Promecotheca nuciferae* Maulik, in

Java. The preoviposition period ranges from three to nine days, and the oviposition capacity of the females varies directly with the size of the females. The normal number of ovarioles is six, but small individuals have a reduced number, resulting in the production of a correspondingly smaller number of eggs. The maximum egg deposition in one day is 18, representing 3 eggs per ovariole; but this occurs only where there has been no opportunity for oviposition for some time previously.

Attack may be upon host larvae in any stage of development from the late first instar onward. Stinging of the larva inhibits further development, but the prepupa is able to complete its transformation. The parasite, however, is able to continue its development upon the pupa provided that feeding begins before the pupal skin hardens. The sex ratio of progeny from small hosts is approximately 1 to 1, and the females predominate from larger hosts.

Cirrospilus ovisugosus C. & M. departs from the normal hyperparasitic habit of the genus in being, instead, predaceous upon the eggs of the four-lined plant bug, *Poecilocapsus lineatus* F. (Crosby and Matheson, 1915). The host eggs are deposited in clusters in plant stems, and the parasite larvae burrows through the pith until it encounters a mass, whereupon three or four eggs are eaten before maturity is attained.

Less extended observations have been made upon a number of additional species of the subfamily. It appears that those which attack leaf-mining larvae, and some others also, usually kill the host at the time of oviposition. This is the habit of a number of species of *Asympiesiella* and *Diaulinus*, whereas *Eulophus viridulus* permanently paralyzes the host instead of killing it. A notable effect, where the host is killed, is the very rapid decomposition of the body, which becomes black, with the contents liquefied, before the short larval feeding period is complete. In *Cratotechus*, however, the host remains active. The eggs of *C. opaculus* Thoms. and *C. longicornis* Thoms. are placed externally, and usually dorsally, and at this point larval feeding takes place. The species that attack hosts contained in mines, tunnels, or cocoons normally place the eggs loosely upon or near the host body.

Practically all species have several generations each year, the number being dependent upon the availability of suitable host stages for attack. Unlike most other Chalcidoidea, the Eulophinae pass the winter mostly in the pupal stage, and this, in some species at least, represents a distinct diapause. In the second generation of *Dimmockia incongruus*, the pupae persist for approximately 10 months, whereas the entire cycle of the first generation averages only 16 days. *Microplectron fuscipennis*, which has already been discussed, is a notable exception to this generalization.

The larvae of this subfamily usually leave the host when feeding is completed and pupate near by. The last larval skin envelops a portion

of the abdomen of the pupa and serves to attach it to the leaf surface or to the wall of the cocoon, mine, or tunnel. The pupal integument is exceptionally heavy, as in the Entedontinae, so that its form is retained after the emergence of the adult. It is at first white but very quickly changes to dark-brown or even to jet black. The pupae either stand erect or, more frequently, lie with the venter upward. The species of *Cratotechus*, which develop on free-living lepidopterous larvae on foliage, leave the host body and often pupate in a circle or ellipse about it, with

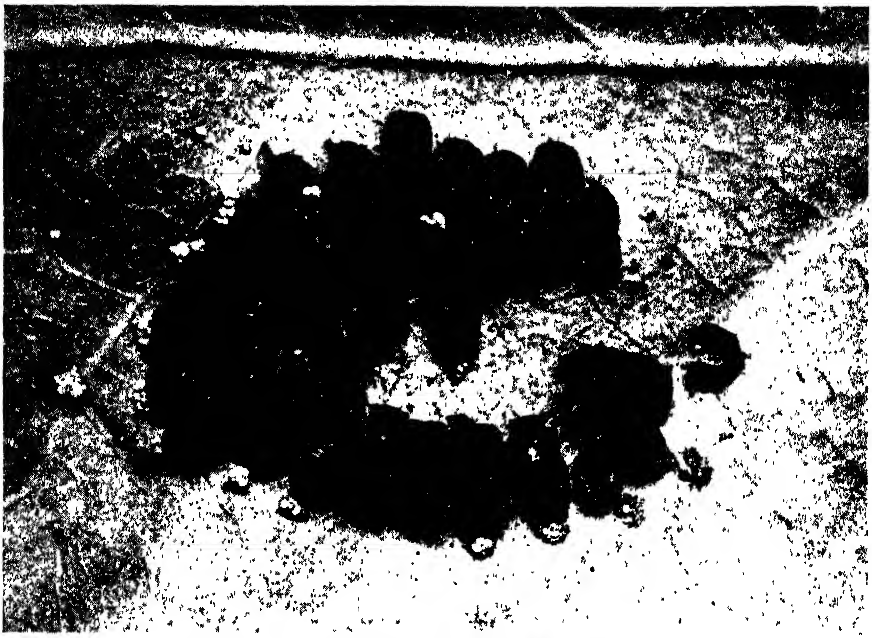


Fig. 60.—A cluster of pupae and pupal skins of *Cratotechus* sp. in characteristic position upon the under side of a leaf. They lie upon the dorsum, with the tip of the abdomen fastened to the leaf surface by the mass of meconial pellets. (*Photograph by Bureau of Entomology and Plant Quarantine.*)

the heads directed toward the center (Fig. 60). Because of this habit, they have been termed "tombstone pupae" by Scudder. Pupation upon foliage without any covering whatever exposes these pupae to heavy attack by hyperparasites, and a high percentage is usually destroyed by other species of Eulophidae and by related families.

Parker and Smith call attention to the occurrence of two color forms among the pupae of *E. viridulus*. Some of those of the summer generation have a relatively thin and brownish-colored skin, whereas that of the overwintering individuals is heavy and black.

Tetrastichinae.—The greater portion of the members of this subfamily develop as internal parasites of the eggs, larvae, or pupae of other

insects. The species of *Melittobia,* with the exception of *M. indicum* Silv., develop externally; they are so highly specialized in their host relationships and habits that they will be discussed separately in a following section.

Tetrastichus is internal, with a few exceptions, such as *T. blepyri* Ashm., which is a hyperparasite of *Pseudococcus* through various Encyrtidae, and *T. radiatus* Waterh., which attacks the nymphs of Chermidae. Urbahns (1917) records an exceptional instance of a parasite developing both as an internal and as an external parasite on the same host. A total of 111 parasitized larvae of the clover seed chalcid, *Bruchophagus gibbus* Boh. (*funebrus* How.), under observation showed 106 bearing *T. bruchophagi* larvae externally and 5 containing them internally.

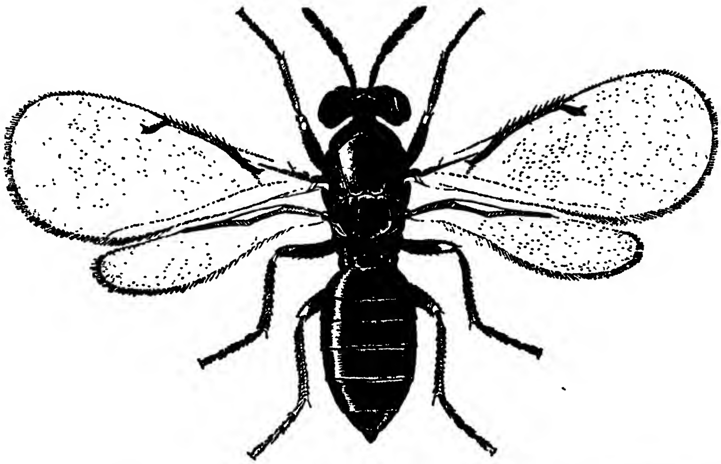


FIG. 61.—The adult female of *Tetrastichus asparagi* Cwf. (*From Johnston,* 1915.)

In a number of species, the greater part of larval development takes place in the host stage following that in which the egg was laid. Thus, *T. asparagi* Cwf. (Fig. 61) oviposits in the egg of the asparagus beetle, but larval feeding is not completed until the prepupal stage in the soil is reached. *T. giffardianus* Silv. and *M. indicum,* which emerge from dipterous puparia, oviposit in the mature larvae just prior to pupation. Voukossovitch (1932) records *T. crassinervis* Thoms. as a primary and secondary parasite of *Hyponomeuta malinellus* Zell. and states that occasional individuals were found even in newly transformed adults, though they were unable to emerge. As a hyperparasite, through *Disochaeta,* the adults are unable to make an emergence hole in the puparium wall and consequently die.

An example of diversity in host relationships within a genus is provided by the species of *Tetrastichus* which are parasitic in Coccinellidae. *T. ovulorum* F. is a solitary internal parasite of the eggs of *Epilachna* in

India, whereas *T. epilachnae* Giard and *T. coccinellae* Kurdj. oviposit in the mature larvae or pupae and emerge only from the pupae. Both species attack the predaceous groups of beetles, and *T. epilachnae* parasitizes the phytophagous *Epilachna*, also.

Although the great majority of species of the subfamily are parasitic in or on the immature stages of other insects, yet several are predaceous in habit. *Ootetrastichus beatus* Perk., which attacks the sugarcane leafhopper, is stated to consume the entire contents of the host egg chamber. *T. schoenobii* Ferr. is recorded by Pagden as being predaceous on the eggs of *Schoenobius incertellus* Wlk. in Malaya, and the larvae also feed upon the young host larvae, which may remain beneath the egg mass for several days after hatching. In *T. verrucarii* Balduf, which is parasitic upon the larvae of Cynipoidea, the larva may move from one gall to a contiguous one and consume the larval occupants. *T. eriophyes* Taylor is normally predaceous in its larval stage and is largely limited for food to *Eriophyes ribis* Westw., which occurs upon currant buds.

Certain members of the subfamily, such as *Melittobia indicum*, have a considerable number of mature eggs in the reproductive system at the time the female emerges, and oviposition takes place immediately, whether or not mating has been accomplished. It is probable that many species are able to do likewise. *M. acasta* Wlk., on the contrary, has a gestation period of 11 or 12 days.

The feeding by adult females upon the body fluids of the host, as in the species of *Melittobia*, has no appreciable effect upon the host individual and does not contribute to a reduction in the population. The first observation of the habit of adult female parasites of feeding upon the body fluids of the host that exude from an ovipositor puncture was that by Marchal (1905) upon *T. xanthomelaenae* Rond., which attacks the eggs of the elm leaf beetle. In some species of *Tetrastichus* and other genera, however, feeding by the adults may destroy a greater number of hosts than is brought about by direct parasitization. Johnston (1915), in discussing *T. asparagi*, records that 71 per cent of 2,000 host eggs examined had been eaten by the parasite females. Eggs in which oviposition takes place are not utilized for feeding. Several true egg parasites of the same genus have been noted to feed similarly. The habit is thus identical with that found in the ichneumonid, *Diplazon laetatorius* F., which reveals also a parallelism in its host relationships. The female of *T. coccinellae* feeds upon the fluids that exude from the wound made in attacking coccinellid larvae. An occasional species constructs a feeding tube.

In oviposition upon exposed hosts, the female usually stands upon the body and inserts the ovipositor perpendicularly. This, however, is often not possible if the host is in an active stage, and insertion is then

made by a forward thrust between the legs. *M. indicum* inserts the ovipositor in the posterior region of the abdomen of the active trypetid larva and may be dragged about by it. These females often burrow into decaying fruit in search of their victims; this is true, also, of *T. giffardianus*. The manner of oviposition of *T. radiatus* on nymphs of (*Euphalerus*) *Diaphorina citri* Kuway. has not been described, but the eggs are placed on the ventral side of the body near the juncture of the thorax and abdomen (Husain and Nath, 1924). In *Thripoctenus russelli* Cwf., which attacks early-stage thrips, the abdomen is curved beneath the body and the ovipositor is inserted near the caudal end, whereas in *T. brui* the female turns about and inserts it by a backward thrust into the lateral margin of the thorax. Marchal concludes that the repeated insertion of the ovipositor by *Tetrastichus xanthomelaenae* into elm-leaf-beetle eggs may be for the purpose of disorganizing the contents and preventing further embryonic development.

Tetrastichus rapo Wlk., an indirect secondary parasite of *Ascia* and other Lepidoptera through *Apanteles*, *Microgaster*, *Anachaetopsis*, etc., places its eggs in the body of its primary host while the latter is still within the living caterpillar. The latter is usually in its last instar at this time. The *Tetrastichus* female is apparently able to determine whether or not the active caterpillar contains a parasite larva and can do so without inserting the ovipositor. This host relationship was first noted by Martelli (1907) and later verified by Gautier and Bonnamour (1924) and Faure (1926). Young caterpillars that are stung by the parasite often die, apparently as a result of mechanical injury, though no eggs are deposited. The species may also serve as a direct parasite of the larvae and pupae of the above Braconidae in their cocoons.

Syntomosphyrum glossinae Waterst., which attacks the pupae of the tsetse-fly, also develops as a hyperparasite through *Mutilla;* when in this latter role, the female reopens the perforation made in the puparial wall by *Mutilla* by means of the hard pointed tip of the abdomen and oviposits through it.

In a great many species of endoparasitic habit, the female deposits the full quota of eggs for development in a single host at one insertion of the ovipositor. *T. giffardianus* deposits an average of eight in each host larva attacked; and *Melittobia hawaiiensis* Perk., when attacking dipterous puparia, deposits approximately 20 in each batch, and the female may remain with the ovipositor inserted for many hours.

Information on the reproductive capacity is available for several species of *Melittobia;* the deposition of 1,086 eggs by *M. acasta* is the maximum recorded. The number of eggs per day in several species of the genus ranges from 30 to 70. A female of *Thripoctenus russelli* deposited 38 eggs in a period of one hour.

It has been noted by Faure (1926) that the eggs of *Tetrastichus rapo* are often found in the anal vesicles of *Apanteles* and *Microgaster*. At deposition, they are placed only in the general body cavity; but apparently they float free in the body fluids and eventually lodge in the vesicle, where the blood circulation is more sluggish.

In spite of the extensive studies made upon this subfamily, relatively little has been reported regarding the habits of the larvae. This presumably is because of a lack of any specialization or departure from normal that may be subject to comment.

The mature larva of *T. ovivorax* Silv., which develops in *Oecanthus* eggs, has the unusual habit, for an egg parasite, of emerging from the empty shell for pupation externally. Pupation of those species of the family which develop internally in larvae or pupae may be either within the body of the host or outside it. The mature larvae of *T. asparagi* emerge from the *Criocerus* prepupa and pupate in the cell that contains it, whereas *T. coccinellae* pupates within the mummified host remains. *T. crassinervis* transforms within the pupa of its lepidopterous host. The mature larva of *T. taylori* Ferr. emerges from the *Elasmus* larva and pupates in the mine of its secondary host; but when development has been in a pupa, or in a larva of *Promecotheca*, the transformation takes place within the empty host skin. The mature larva of *T. radiatus* utilizes the host body as a covering and fastens it to the leaf surface with a few strands of silk just prior to pupation, a habit comparable with that of a number of species of Elachertinae upon caterpillars. The species of *Thripoctenus*, which attack thrips, slough off the host skin but retain it as a crumpled mass enveloping the tip of the abdomen of the pupa.

A considerable number of species are solitary in habit, this being true particularly among the egg parasites and those of the genus *Thripoctenus* developing in thrips. Even among the former, however, there are some that produce two or three individuals in each host egg. Among those attacking larvae and pupae, the maximum recorded is 338 *Melittobia hawaiiensis* upon a single larva of *Sceliphron*, though Gater (1926) secured 119 of what is presumably the same species (recorded as Chalcid No. 1594) from a puparium of *Ptychomyia remota* Ald. in Malaya. Only five or six *Tetrastichus asparagi* develop in each asparagus-beetle larva, and an average of eight *T. giffardianus* in pupae of the Mediterranean fruitfly.

The life cycle of the Tetrastichinae is relatively short in all species. The minimum period required for development from egg to adult is 6 to 10 days recorded for *Tetrastichus ovulorum* in India. The great majority complete the cycle in 15 to 25 days. Buckell (1928) records an exceptionally large difference in the time required for the development

of the two sexes of *Melittobia chalybii* Ashm. under experimental conditions. The males require only 21 days as compared with 37 days for the female.

Due to the short life cycle, there is the possibility of a considerable number of generations each year. Some are restricted to a single generation each year corresponding to that of the host, but most species have two or three. *T. xanthomelaenae* has nine generations each season in Italy. This species is able to reproduce continuously during the entire period in which elm-leaf-beetle eggs are available in the field. An exceptional adaptation to the life cycle of the host is shown by *Thripoctenus brui* Vill. which in northern Europe has a single generation annually, corresponding to that of the host, *Kakothrips pisivorus* Westw., whereas in Japan there are four or five generations upon *Thrips* and *Taeniothrips*, which themselves have a number of generations each season.

Hibernation usually takes place in the mature larval stage in the host body or in the cell which it occupies. A portion of the brood of *M. acasta* may pass the winter in the pupal stage. The hibernation habit of *Tetrastichus xanthomelaenae* has not been positively determined; but no alternate hosts are known, and it is presumed that the adult females persist in sheltered places until the following spring. *Thripoctenus russelli* and *T. brui* pass the winter period in the pupal stage. Under certain conditions, the immature stages of the Tetrastichinae may go into diapause for an extended period. Giard (1896) records collecting parasitized pupae of *Epilachna* containing *Tetrastichus epilachnae* in September and holding them in a heated room until the following July; at this time, many of the parasites were still in the mature larval and pupal stages.

The sex ratio of practically all species of the subfamily shows a marked preponderance of females. In all species of *Melittobia* that have been studied, the females predominate in the ratio of 9 to 1 or more, the extreme being 31 to 1 in *M. hawaiiensis* when developing on hymenopterous larvae in Hawaii. *T. crassinervis* and *Tetrastichus* sp. from elm-leaf-beetle eggs in Japan are the only species in which the sexes occur in approximately equal numbers.

Normal unisexual reproduction occurs in *T. asparagi*, *Ootetrastichus beatus*, *Thripoctenus russelli*, and *T. brui*. The occurrence of this mode of reproduction in *T. brui* in Europe is of interest, for Sakimura's (1937) studies in Japan revealed the presence of both sexes, the females predominating 3 to 2.

Melittobia.—The host relationships and habits of several species of the genus *Melittobia* have been studied in detail by several authors. *M. acasta* Wlk. has been dealt with by Howard and Fiske (1911), Graham-Smith (1919), Picard (1923), Balfour-Browne (1922*b*), and Parker and

Thompson (1928). Accounts have also been given of *M. chalybii* Ashm. by Buckell (1928) and in more detail by Schmieder (1933, '38). These and other species of the genus are very similar in habit.

M. acasta is recorded from a wide variety of hosts and may be either primary or hyperparasitic in its relationships. As a primary external parasite, it is recorded from many Hymenoptera, particularly Apoidea, and also from Vespoidea, Sphecoidea, etc. In the hyperparasitic role, it attacks the Ichneumonoidea, Chalcidoidea, and Tachinidae. Experimentally (Parker and Thompson), it has been reared upon a number of hosts not attacked under natural conditions, such as coleopterous and lepidopterous pupae and spiders. Development in *Camponotus* pupae was made possible by partial desiccation, resulting in the formation of internal air cavities, which simulated natural conditions for the parasite. Oviposition does not take place in dipterous hosts prior to the hardening of the puparium.

A pronounced sexual dimorphism occurs among the adults of *M. acasta*. The females are of normal form, with all appendages and organs fully developed, whereas the males are without eyes or wings. The males normally do not leave the cell, cocoon, or puparium in which they develop. They transform a few days prior to the females and mate with them immediately after the pupal skin is cast. These males are very pugnacious and fight among themselves until only one remains alive. No feeding has been observed by individuals of this sex. The females, on the contrary, feed very extensively upon the body fluids of the host and, when necessary, construct a feeding tube for this purpose. This feeding does not affect the host sufficiently to interfere in any way with the later development of the brood upon it.

In oviposition, the ovipositor may be thrust through the host envelope; or, if this is thin, the female may bite away a hole and enter the cell of the host larva. In the Hymenoptera, the mature larva only is attacked; it is usually stung into immobility prior to oviposition. According to Picard, the host larvae are killed by the sting, and they may remain in a suitable condition for feeding by the parasite for a period of eight or nine months. Parker and Thompson state that form and color have no significance as oviposition stimuli; imitation cocoons smeared with host blood do not attract the parasites. The number of eggs placed on a host is regulated somewhat according to its size.

The normal sex ratio of the progeny of mated females shows a great preponderance of females, with the males representing only 1 to 5 per cent of the total. Virgin females deposit a much reduced number of eggs, this being approximately equal to the total number of male progeny in a normal brood. No further oviposition takes place until mating is accomplished, and this may be, if necessary, with one of the female's own

male progeny from the small number of eggs already laid. The unmated female takes a marked interest in these few developing progeny, frequently stroking them with the antennae, and her interest is accentuated when the pupal stage is reached. No other instance of maternal care or interest in the progeny is known among the Chalcidoidea. Balfour-Browne secured an average of 35.6 eggs from each unmated female of a series, the total period extending to 225 days; but this relatively large number was induced by the removal of the eggs as soon as laid. Even with the abdomen distended with eggs, the female will refuse to deposit a further number. If then mated, she will proceed immediately to the deposition of the full quota, of which the usual small portion produce male progeny. Frequently, however, the supply of spermatozoa in the spermatheca is not adequate for the fertilization of the entire quota of eggs, and consequently repeated mating is necessary. As both sexes are produced after mating, "it is reasonable to conclude that she can control the flow of spermatozoa from her spermatheca and thus determine the sex of her offspring."

The reproductive capacity of *M. acasta* is very high, the maximum number of eggs recorded from a single female being 1,086. In this instance, oviposition extended over a period of approximately three months, and the daily maximum was 31. Unmated females may live four months or longer, so that there is sufficient time available for the development of a brood of male progeny and for normal oviposition after mating with one of them.

Two to five or more generations may be produced each year, and two successive broods may develop upon a single host larva. The cycle from egg to adult covers a minimum of about 17 days, of which 2 days are required for incubation of the egg, 8 days for larval development, and 7 days for the pupal stage. The winter is passed in the mature larval or pupal stage in the host envelope or cell.

In *M. chalybii*, which has been studied in detail by Schmieder, there are a number of departures in habit from those of *M. acasta*. The host preferences are virtually identical, but the females are stated to enter the host cell before it is sealed or to attack the larva before the cocoon is spun. The adults reveal a polymorphism in form comparable with that in social bees and wasps. The type form of the male is light-brown in color; it has well-developed ocelli, and the eyes are represented by a black ocellus-like spot on each side. In the second form, the ocelli may be absent or vestigial, the eyes unpigmented, the wings smaller, and the body color dark reddish-brown. The type form of the female is brownish-black, and the wings are fully formed; the second form is brown in color and has crumpled nonfunctioning wings, the ectoskeleton is thinner, the sclerites are less distinctly outlined, and the abdomen is

very large and distended at emergence. The type form completes the cycle from egg to adult in approximately 90 days, and the adults live for 60 to 75 days. In contrast to this, the cycle of the second form is only 14 days, and adult life is shortened to a maximum of 30 days. The type-form females have a gestation period of 11 to 12 days and may deposit a maximum of 500 to 800 eggs, whereas those of the second form oviposit the day of emergence, usually do not feed, and produce only 40 to 60 eggs. Virgin females produce up to 10 eggs only, and most of these do not hatch. Normally, two complete broods develop on each host individual; the first consists of both forms, and the individuals of the second form reach maturity quickly and produce a brood destined to be of the type form, which develops along with the type-form remainder of the first brood.

The winter is passed in the mature second-form larval stage. The type form ensures the dispersal of the parasite, whereas the second form is reproductive only. It was demonstrated experimentally that only type-form females can be produced upon a host after a small number of second-form larvae have developed upon it. This is explained on a nutritional basis. The food of the second form consists mainly of blood, whereas that of the following type form comprises a considerable portion of solid materials.

Usually about 3 per cent of the progeny of mated females are males; and although the proportion is small and is further reduced by combat, yet practically all the females are eventually fertilized. According to Schmieder, "The sex ratio here seems to be an adaptive feature which conserves the food supply of the species for the almost exclusive use of the female sex, the sex which alone serves the dispersal of the species." The males of this species have been found to be haploid, derived from unfertilized eggs of either mated or virgin females, and this condition is generally lethal. There is as yet no evidence for the production of biparental males. Only the very small proportion of eggs indicated possess parthenogenetic potentialities.

Entedontinae.—The most extensive studies on the biology of the Entedontinae are those by Taylor (1937) upon several species of *Pleurotropis* parasitic in the larvae and pupae of *Promecotheca,* and of several other genera associated with this host. *Pleurotropis parvulus* is of special interest, not only because of its habits but from the point of view of effectiveness in the control of the host. It is a gregarious internal parasite of all larval instars and of the pupa as well. The number of eggs deposited in a given host varies directly with its size. Thus, an average of 3 is deposited in first-instar larvae, whereas 17 is the average for third-instar larvae, prepupae, and pupae. The minimum number that can reach maturity in the latter instars is 5, and a lesser number

cannot consume a sufficient portion of the body contents and consequently die.

The reproductive capacity of *P. parvulus* is relatively low, for large females produce an average of 77 eggs and small ones only about 20. An examination of the reproductive system of females of different sizes revealed that the small individuals consistently have smaller and fewer ovarioles, which is reflected in a reduced egg capacity.

The life cycle is complete in 19 to 21 days, of which about 3 days are required for incubation of the egg, and 7, 1, and 9 days, respectively, for the larval, prepupal, and pupal stages.

Several species of the genus *Pleurotropis* develop consistently in the tertiary role (Muesebeck and Dohanian, 1927). *P. tarsalis* Ashm. and *P. nawaii* Ashm. are associated with the gypsy moth and related hosts of *Apanteles*, and they develop upon the various species of secondary parasites that attack the larvae of that genus.

The habits of only a few additional species of Entedontinae are known. According to Bakkendorf (1933), *Anellaria conomeli* Bakk. is an internal parasite of the egg of *Conomelus limbatus* F. during its early larval period, but after consuming the contents of the one egg it emerges and completes its development as a predator. In order to do this, it must bore its way through the pith of the stem containing the host eggs in order to reach them. A total of seven or eight may be consumed before maturity is reached.

Achrysocharella orientalis Ferr., according to Taylor, is a hyperparasite of *Promecotheca* through *Pleurotropis* and *Dimmockia*. It develops internally in the mature larvae or pupae of the primary parasites within the dead body of the coleopterous host. When it is parasitic in *Pleurotropis*, its early stages are internal, and it then emerges and, in the last stage, becomes predaceous upon the remaining individuals of the group within the hispid skin. Larvae that develop in *Dimmockia* do not have this external feeding phase.

Achrysocharis promecothecae Ferr. is parasitic in the eggs of *Promecotheca* in Java. Only eggs at least 10 days old, in which embryonic development is well-advanced, are selected for oviposition. Occasionally, a parasitized egg may hatch, and in that case the parasite completes its development in the first-instar larva in the mine. The adults do not emerge through the exposed portion of the egg capsule but, instead, through the ventral side and through the epidermis of the leaf.

The pupation habits of members of the subfamily present several points of interest. Howard (1891) describes an unusual adaptation in *Chrysocharis singularis* How.,[1] a parasite of the larva of *Lithocolletis* in

[1] A. B. Gahan states that this is a *nomen nudum* and that the species dealt with is probably not of that genus.

its leaf mine. The mature larva of the parasite builds a series of "pillars" in a circle about its body, and these serve to hold the walls of the mine apart and thus protect the pupa after the molt. These pillars may possibly be formed of the larval meconium, though they are said to be more probably derived from regurgitated material.

The pupal integument of most species is exceptionally heavy and black in color, and, after emergence of the adult, the exuviae retain the pupal form, rather than becoming a crumpled mass or being broken into fragments, as is usually the case in the Chalcidoidea.

The life cycles of the members of the family are relatively short, usually being completed in 15 to 20 days, of which half is passed in the pupal stage. *Pleurotropis tarsalis* requires 28 to 40 days, of which the pupal stage covers the exceptionally long period of 18 to 26 days.

Bisexual reproduction is normal for the subfamily, and no conclusively proved instances of unisexual reproduction are known. In the great majority of species, the females predominate in numbers. The ratio ranges from 1.6 to 1 in *P. metallicus* Nees to 3 to 1 in *P. benefica* Gahan (Salt, 1931), 2 to 1 in *Achrysocharella orientalis*, and 7.4 to 1 in *Achrysocharis promecothecae*. The ratio in *P. parvulus* is dependent upon the host stage attacked. From first-instar *Promecotheca* larvae, the females predominate in the ratio of 1.7 to 1, whereas the excess of that sex from third-instar larvae and pupae is 4.3 to 1. Irrespective of colony size, there is almost invariably at least one male in the group.

Elachertinae.—Extended observations on *Euplectrus plathypenae* How. of North America have been made by Swezey (1924), R. C. Smith (1927), Vickery (1929), and Wilson (1933). It is a gregarious external parasite of the half-grown or larger larvae of various Noctuidae, particularly *Laphygma* and *Cirphis*, in North America. The characteristic clusters of closely packed larvae upon the body of the host (Fig. 62) make it readily recognizable. A maximum of 45 may develop on a single *Laphygma* larva.

The adults are relatively long-lived but begin ovipositing within a day or two after emergence. Swezey records the deposition of 213 eggs by a single female in a period of two weeks. Eggs are not deposited on host larvae about to molt. In the act of oviposition, the female stands upon the body of the host, usually on the dorsum of the thorax or of the first two abdominal segments, and the eggs are placed in groups not closely spaced, and at times in rows, upon the integument, to which they are firmly attached (Fig. 63*B*). The host is not paralyzed at the time of oviposition. This position gives the least chance of the female being dislodged during oviposition and of the young larvae being injured while the host is still active.

The egg is white in color when first laid but changes to brownish-black or black as incubation progresses. Hatching takes place in about two days and is accomplished by a longitudinal splitting of the chorion along the median dorsal line. Feeding begins immediately, and the body gradually enlarges and emerges from the eggshell. The shell remains as a ventral pad, which attaches the larva to the host, and to it the successive exuviae are added. In the early stages, the larvae may not be contiguous; but as growth proceeds they become greatly crowded, causing a noticeable compressing of the anterior portions of the body, and the individuals in the center of the cluster are in a vertical position. According to Smith, the host larva dies at the time the eggs hatch,

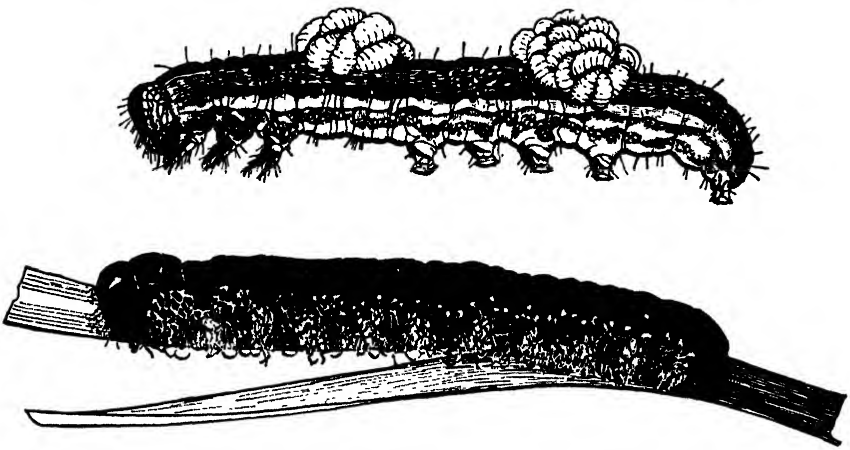


FIG. 62.—Host larva bearing two clusters of larvae of *Euplectrus plathypenae* How. on the dorsum, and (below) showing the loosely spun parasite cocoons arranged transversely beneath the body of the caterpillar. (*From Swezey*, 1924.)

whereas Swezey and Wilson record that the parasite larvae may complete their feeding before the death of the host. It is probable that the effect is not uniform upon all host species and stages.

The body contents of the host are very largely sucked out; the larvae, after the completion of feeding, leave their position on the dorsum and find their way beneath the host, where they arrange themselves transversely and spin delicate cocoons within which to pupate (Fig. 62). These perhaps are improperly termed cocoons; they are merely thin webs of silken strands which fasten the ribbon-like host skin to the leaf surface and partition off the pupae each from its neighbors.

The life cycle is very short, ranging from 10 to 15 days under summer temperatures, with the egg, larval, and pupal stages requiring 2, 4 to 6, and 4 to 7 days, respectively. Wilson records a sex ratio of 1.5 to 1, the females predominating, in the third brood and 9.2 to 1 in the sixth brood. Parthenogenetic reproduction results in male progeny only.

The early observations on *E. comstocki* How., a parasite of the cotton leaf worm, by Schwartz (1881) indicate that its habits are quite similar to those of *E. plathypenae.* The host is attacked in a relatively early stage, when it is less than one-third grown, and the eggs are placed upon the middle of the back rather than upon the thorax.

E. bicolor Swed. of Europe, which attacks caterpillars of a considerable number of species, has been studied by Silvestri (1910*c*), Thomsen (1928), and Bischoff (1929). According to Silvestri, the number of eggs placed upon an individual host varies directly with the size of the latter. Oviposition is very rapid, and the eggs are placed at 1-mm. intervals on the dorsum between the mesothorax and the fourth abdominal segment.

More recently, Noble (1938*a*) has given a detailed account of the Australian *E. agaristae* Cwf., which is parasitic upon the caterpillars of the grape vine moth, *Phalaenoides glycine* Lew. A maximum of 60 may attain maturity upon a single host, though the average is about 18. In case of superparasitization, all individuals of the brood continue feeding without combat until the food supply is exhausted, following which all may die or develop into dwarf adults. The winter is apparently passed in the adult stage, and fertilized females have survived for six months under insectary conditions.

The habits of the genus *Elachertus* differ appreciably from those of *Euplectrus* which have just been discussed. One species of the genus (listed as Chalcid sp. B., Tothill *et al.*, 1930) is a solitary external parasite of the caterpillars of *Artona trisignata* in Java. The female often feeds on the body fluids of the host, and this is always fatal to the latter. At the time of stinging, a fluid is pumped into the host body by the female, causing a marked distention. The ovipositor remains inserted for 10 minutes or more, following which the female bites a hole in the integument of the thorax and sucks out the body fluids. The single egg is placed dorsally between the first and second abdominal segments. Immediately after hatching, the young larva moves to the ventral side of the host body and takes up its feeding position between the thoracic and abdominal legs. When more than one egg is deposited on a host, the hatching of one causes the immediate cessation of development of the remainder. "Apparently the young larva injects into the host some fluid which is toxic to the other eggs, and this fluid then reaches the latter by diffusion through the egg stalks." This explanation has often been given for the death of surplus individuals among internal parasites and is particularly plausible in those species which show appreciable growth of the egg during incubation as a result of taking up fluids from the surrounding medium. In *Elachertus*, however, only the pedicel of the egg is within the host body, and this, unless it comprises the

micropylar area, which is improbable, would not provide a channel through which diffusion might take place.

The host is temporarily paralyzed at the time of oviposition, and its activities cease completely when the egg hatches. Liquefaction of the body contents starts immediately and is ascribed to the injection of some fluid into the body by the parasite larva. If this is true, the effect is in contrast to the preservative action of the fluids injected by the sting of many other parasites, and therefore this injection is for a directly opposite purpose.

Elachertus affinis Masi (Silvestri, 1910*c*) is a European parasite of the mature larva of *Polychrosis ambiguella* and differs somewhat in habit from the above species. The eggs, to the number of 5 or 10, are placed within the host cocoon but not directly upon the body of the larva, and the latter is not paralyzed. The young larvae are very active and are able to move about freely in the cocoon. The life cycle is completed in 11 to 13 days at summer temperatures.

Trichospilus pupivora Ferr. differs in habit from the genera already discussed, it being a gregarious internal parasite of the pupae of the palm caterpillar, *Nephantis serinopa* Meyr., in India (Anantarayanan, 1934). An average of 55 eggs is laid in each pupa, and a maximum of 211 individuals has been reared from a single host.

The pupation habit of *Euplectrus* is particularly interesting. When the larvae finish feeding upon the host and have completely sucked out the fluid contents, they leave the dorsal position and seek the underside of the deflated host body, where they arrange themselves transversely, in a single orderly row in some species, and prepare for pupation. A light web-like cocoon (Fig. 62) is formed which binds the host remains to the leaf surface, and the latter thus serves as a protective covering. Several authors have called attention to the fact that the material from which this cocoon is spun is derived from the Malpighian tubes rather than from the salivary glands and that the slender tapering tip of the abdomen of the larva serves as an "arm" in its construction. The meconium is cast by the prepupa, and, in some species at least, it is ejected from the cocoon. The pupa lies upon its dorsum and is attached to the substratum by means of the last larval exuviae, which envelops the tip of the abdomen.

In *Elachertus* sp., studied by Tothill *et al.*, the solitary larva likewise pupates beneath the host skin, and the pupa lies upon its back with the spiracular processes directed upward. These "hooks" are considered to serve a protective purpose in holding the host remains away from the body to permit of normal respiration. The collapsed host remains envelop the pupa closely, and the spiracles at the tips of the hooks are believed to be the only ones that function.

According to Howard (1891), the pupa of *Elachertus cacoeciae* How. is attached by the tip of the abdomen to the silk spun in the leaf roll by its host, *Archips rosaceana* Harr., whereas those of *E. spilosomatis* How. are found in a group among the long hairs on the dorsum of the abdomen of the larvae of *Diacrisia virginica* F.

IMMATURE STAGES

The eggs of the great majority of Eulophidae are simple; they are oblong or ovate to elongate, are often slightly arched, and have both poles smoothly rounded. The chorion is usually delicate and unsculptured, though in *Microplectron fuscipennis* it shows, under high magnification, minute, conical projections. In a number of species, the micropyle is distinguishable as a small thickened area at the anterior end.

The eggs of several genera of Elachertinae differ from those of the majority of the members of the family. Those of *Euplectrus* and *Elachertus* have been stated by several authors to have a pedicel at the middle of the mid-ventral curve; this serves as

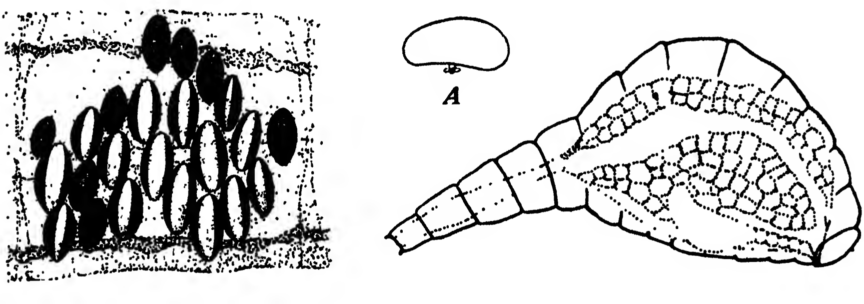


FIG. 63.—Immature stages of the Eulophidae. *A*, the egg of *Euplectrus bicolor* Swed., showing the median ventral pedicel (*from Silvestri*, 1911); *B*, a cluster of eggs, some partially hatched, of *E. plathypenae* How. (*from Smith*, 1927); *C*, the mature larva of *E. agaristae* Cwf. (*from Noble*, 1937).

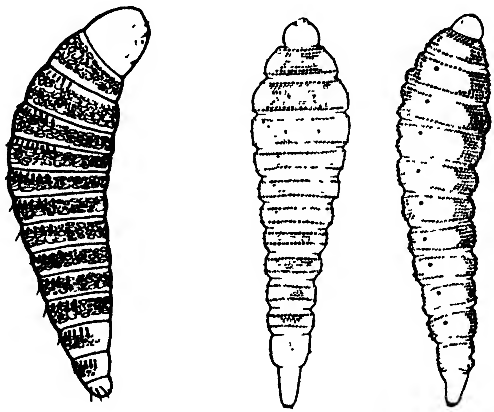
an anchor in the skin of the host in the same manner as with the pedicellate eggs of other groups. Observations regarding its form and origin are incomplete. In the figure given by Silvestri for *Euplectrus bicolor* (Fig. 63*A*), the pedicel appears to be a definite adaptive modification possibly comparable to that of the tryphonine Ichneumonidae, and Tothill states that it is "continuous with the egg shell" in *Elachertus* sp. It may prove, however, to be similar in origin to those of *Euxanthellus* and the male eggs of some *Coccophagus*, in which a fold of the unmodified chorion is knotted or twisted at the time of deposition and is inserted into the puncture in the host skin. An examination of the ovarian egg would probably clarify this point.

The pronounced darkening of the chorion of the egg during incubation, which occurs in *Euplectrus plathypenae* (Fig. 63*B*) and *E. comstocki*, has not been observed in other species of the family.

Records of the number of larval instars of the different species show little consistency. Only three have been detected in *Eulophus viridulus* and *Melittobia acasta*, four in *Pleurotropis parvulus*, *Tetrastichus ovivorax*, and *Euplectrus bicolor*, and five in *Microplectron fuscipennis*.

The first-instar larvae are hymenopteriform and somewhat cylindrical, with 13 distinct body segments, and they have no characters to distinguish them readily from

larvae of related families. Occasional species bear fleshy protuberances or tubercles on the body. In *Diaulinus* sp. (*Solenotus* sp.) figured by Parker (1924), the sensory setae are borne upon distinct tubercles. The larvae of *Dimmockia javana* possess distinct intersegmental protuberances, which function as pseudopodia, on the mid-ventral line from the second to the ninth body segments. Each segment bears a transverse row of minute setae on the dorsum and sides near the posterior margin. The last abdominal segment is bifurcate in *Tetrastichus* sp. (Berry, 1938); this species has been confused with *T. xanthomelaenae* from the same host, but the latter does not possess this character. *Melittobia acasta* has a row of minute spines at the anterior margin of each segment, and *T. taylori* has a double row in the same position. In *T. ovivorax* (Fig. 64*A*), this row of spines occurs only dorsally on each segment except the first, and in the *Tetrastichus* sp. mentioned above they encircle the segments. According to Silvestri (1910c), the row of spines occurs at the posterior margin of the segments in *T. xanthomelaenae*. *P. parvulus* apparently lacks the sensory setae and cuticular spines.



A B

FIG. 64.—*A*, the first-instar larva of *Tetrastichus ovivorax* Silv. (*from Silvestri*, 1920); *B*, mature larva of *Hyperteles intermedia* Thoms. (*from Parker*, 1924).

The integument of a number of species bears a distinct sculpturing. That of *T. ovivorax* has a pebbled appearance, whereas in *T. xanthomelaenae* it is imbricated. *Hyperteles intermedia* Thoms. (Parker and Thompson, 1928) has irregular areas of minute tubercles on all body segments except the last two. There are three pairs of sensory tubercles on each thoracic segment and four pairs on each abdominal segment except the last, which has only one.

The majority of species that have been studied have an open tracheal system, with spiracles on the mesothorax and the first three abdominal segments. *Euplectrus bicolor* is said to have five pairs, the additional one being on the metathorax. Several species of endophagous habit lack the open tracheal system, among them being *P. parvulus*, *Tetrastichus taylori*, *Anellaria conomeli*, and *Thripoctenus brui*.

The distinguishing characters of the first instar, particularly the cuticular spines and ornamentation, usually do not persist after the first molt, and the intermediate larval instars of the different species are consequently quite similar. In *Diaulinus*, however, the tubercles and setae are retained to the final instar, and this is true, also, of the two pairs of "papillae" on the last abdominal segment of *Eulophus viridulus*.

In most species, the full complement of nine pairs of spiracles, situated on the last two thoracic and the first seven abdominal segments, appears in the second instar. They are stated to be on the mesothorax and the first eight abdominal segments of *Melittobia acasta*.

The mature larvae are usually of simple form, with very few integumentary spines or setae, and are usually without surface sculpturing. *Tetrastichus eriophyes* bears transverse striations, whereas *T. ovivorax* has the minute tubercles, mentioned for the first instar, ventrally. The larva of *H. intermedia* (Fig. 64*B*) bears numerous small integumentary tubercles in transverse rows both ventrally and dorsally on all body segments except the last. In *Thripoctenus brui*, the mature larva differs considerably from that of other genera in being cylindrical and about three times longer than wide, with both ends broadly rounded and no visible segmentation; it bears a transverse ring of about 12 short but stout spines at the middle of the body. The mandibles of *Tetrastichus ovivorax* are bidentate, in contrast to the simple form of other species of the family.

The larvae of the gregarious species, such as *Euplectrus* (Fig. 63*C*) upon free-living hosts, are pear-shaped and are very broad in the mid-abdominal region; the last four or five segments are much narrowed.

Nine pairs of spiracles are usually present, these being on the last two thoracic and the following seven abdominal segments. *Pleurotropis benefica, P. parvulus*, and *Chrysocharis laricinellae* Ratz. have only seven, those on the third thoracic and on the first abdominal segments being missing. In *P. parvulus*, the number is said to be variable, usually smaller than the full complement mentioned, and it may differ on the two sides of the same individual. *Thripoctenus brui* and *Anellaria conomeli* lack the spiracles even in the mature larva, and Silvestri does not mention or figure them in *Tetrastichus ovivorax*.

The pupae of a considerable number of species, particularly of the Eulophinae, have an exceptionally heavy integument which may be jet black or dark-brown in color. In a species of *Elachertus* found attacking *Artona* by Tothill, the pupa bears a pair of fleshy processes at the lateroventral margins of the seventh and eighth abdominal segments, each of which bears a spiracle at its tip.

APHELINIDAE

The family Aphelinidae is a relatively large group, the species of which are most frequently encountered as primary parasites of the homopterous families Coccidae, Aphididae, and Aleyrodidae. The more common and well-known genera that develop internally are *Aphelinus* in Aphididae, *Coccophagus* and *Aneristus* in lecaniine Coccidae, *Prospaltella* in diaspine Coccidae and Aleyrodidae, and *Encarsia* and *Eretmocerus* in Aleyrodidae. The species of *Aphytis* are ectophagous parasites of diaspine Coccidae, and the larvae of several have been found to feed also upon the eggs of their hosts.

In addition to the host groups mentioned above, there are a number of records upon other orders and families. *Centrodera xiphidii* Perk. parasitizes the eggs of a locustid, *Xiphidium varipenne* Swezy, in Hawaii and has been reared as an internal parasite of the mature larvae of *Haplogonatopus*, a dryinid parasite of leaf hoppers. *C. cicadae* Silv. develops in the eggs of *Cicada plebeja* Scop. in Italy, and *Centrodera*

speciosissimus Gir. is an internal parasite of the larvae and pupae of the hessian fly in North America.

In a hyperparasitic role, the Aphelinidae may be found attacking the mature larvae and pupae of various members of their own family and of other Chalcidoidea within the remains of their hosts. *Ablerus* is perhaps the best known genus having this habit. *A. clisiocampae* Fitch is at times reared abundantly from the eggs of the eastern tent caterpillar, *Malacosoma americana* F., while *A. macrochaeta* var. *inquirenda* Silv. destroys approximately 50 per cent of the various primary species that attack *Aleurocanthus* spp., in tropical Asia. *Marietta* (*Perissopterus*) is often found associated with a wide variety of Coccidae, and Compere expresses the opinion that all members of the genus are of hyperparasitic habit. The male progeny of several species of *Coccophagus* develop only as hyperparasites, whereas the females are primary parasites.

A number of species of Aphelinidae have been of great value in the biological control of their hosts. Those which have been credited with effective control in one or more countries are as follows:

Parasite	Host
Aphelinus mali Hald.	*Eriosoma lanigerum* Hausm.
Aspidiotiphagus citrinus Craw	*Aspidiotus destructor* Sign.
Coccophagus gurneyi Comp.	*Pseudococcus gahani* Green
Encarsia formosa Gahan	*Trialeurodes vaporariorum* Westw.
Eretmocerus serius Silv.	*Aleurocanthus woglumi* Ashby
Prospaltella berlesei How	*Aulacaspis pentagona* Targ.
Prospaltella smithi Silv.	*Aleurocanthus spiniferus* Q.

BIOLOGY AND HABITS

Extended studies have been made upon a number of species of the family, the more important being as follows: Lundie (1924) upon *Aphelinus mali* Hald.; Hartley (1922) upon *A. semiflavus* How.; Taylor (1935) upon *Aphytis chrysomphali* Mercet, *Physcus intermedia* Gahan, and *Casca parvipennis* Gahan; Imms (1916) and Griswold (1925) upon *A. mytilaspidis* LeB.; Clausen and Berry (1932) upon *Eretmocerus serius* Silv.; and Cendaña (1937), Flanders (1936, '37), and Smith and Compere (1926, '28) upon a series of species of *Coccophagus*.

The species of the family which are parasitic upon Coccidae generally limit their attack to the females, doubtless owing to the greater size of the individuals of that sex. The cosmopolitan *A. chrysomphali*, however, attacks not only the female scales but the male prepupae and pupae also. Schweig and Grunberg (1936), on the contrary, state that the attack is limited to the male scales of *Chrysomphalus aonidum* L. in Palestine and that a parasitization of 70 to 80 per cent results in some reduction in the infestation through lack of fertilization of a portion of the females. Taylor mentions that both sexes of *Aspidiotus destructor*

Sign. are attacked by *Aspidiotiphagus citrinus agilior* B. & P. and *Casca parvipennis* Gahan. In *Aphytis chrysomphali*, which attacks many species of diaspine Coccidae, the order of preference is said to be related directly to the thinness of the scale covering.

An unusual adaptation is found in *Coccophagus gossypariae* Gahan, a North American parasite of the European elm scale, *Gossyparia spuria* Mod., wherein the first generation develops only in male scales and the second in the mature females (Griswold, 1927). The adults of the second brood are of larger size as a result of the greater amount of food material available to the larvae.

There is a considerably greater latitude in the stage of host development suitable for attack by Aphelinidae than is found in many other groups. According to Hartley the younger aphids are preferred by *Aphelinus semiflavus;* yet attack is successful upon all stages, from those newly born to the adults. The development of *Aphytis chrysomphali* on both male and female *Aspidiotus* has already been mentioned, but it may be noted that a decided preference is shown for mature females, including those which have begun oviposition. Griswold states that the first generation of *Aphytis mytilaspidis* develops upon second-instar *Aspidiotus*, etc., the second generation upon the mature females, and the third either upon these or upon the eggs. The species of hyperparasitic habit limit themselves mainly to the mature larvae and pupae.

In a number of species of *Coccophagus*, there is a sex differentiation in host relationships of a complex and varying nature. A discussion of this phenomenon will be given in a later section, and that portion of the following account which relates to reproduction is restricted to the groups of the family in which the habits are simple and both sexes develop in the same way.

Habits of the Adult.—The species of the family that are parasitic in aphids effect emergence through a circular hole cut dorsally in the integument of the host remains near the posterior end of the body. *Coccophagus* spp. in lecaniine scales makes the emergence hole in the same position. *Casca parvipennis*, after developing in second-instar *Aspidiotus*, emerges at the anterior end. *Eretmocerus* and *Prospaltella*, parasitic in *Aleurocanthus*, likewise emerge through a hole at the anterior end of the body. *Aphytis chrysomphali*, an external parasite, has a variable emergence habit. In *Chrysomphalus aonidum*, it cuts a hole or slit in the dorsum of the scale covering, and the flap thus formed is forced outward like a trap door. In male scales and in the females of species such as *Aspidiotus destructor*, which have delicate coverings, the parasite often emerges by merely pushing its way out from beneath the margin. Because of this habit, a count of emergence holes is not a satisfactory basis for determining the extent of parasitization.

The majority of species probably derive their food during the adult period from the honeydew secretions of their hosts. In *Aphelinus*, however, a considerable number of species feed upon the fluids that exude from an ovipositor puncture in the body of the host. This feeding may result in the death of the aphid host, and Hartley states that *A. semiflavus* may be as effective in the role of a predator upon *Myzus persicae* Sulz. as in its parasitic capacity. A single female ordinarily kills three or four small nymphs each day by such feeding. *Aphytis chrysomphali* feeds at wounds made in the host body, but in this instance the puncturing of the host body has no relation to oviposition, for the latter act does not involve stinging. Quayle records an unusual feeding habit in *Coccophagus lycimnia* Wlk., in which the females gouge out narrow strips of leaf tissue with the mandibles. Candaña describes in detail the feeding of the females of *C. scutellaris* Dalm. upon honeydew given off by scale insects. This habit is developed to such an extent that the parasite strokes the host with its antennae, very much as it is done by ants, to induce it to excrete a drop of fresh honeydew, which is immediately eaten.

The species that are primary parasites of Aphididae and Aleyrodidae insert the ovipositor by a backward thrust, and consequently the female does not stand upon the host in depositing her eggs. The external parasites of Coccidae usually place the egg beneath the body of the scale and adhering to the integument, though some may be placed dorsally but beneath the scale covering. In *A. mytilaspidis*, the latter position is stated by Griswold to be the most common upon mature females, whereas the egg is usually found ventrally upon second-instar larvae. *Eretmocerus serius*, an internal parasite of *Aleurocanthus*, thrusts the ovipositor completely through the host body from the dorsolateral region, and the egg is deposited upon the leaf surface beneath the body. According to Compere, the female of *Coccophagus saintebeauvei* Gir. consistently inserts her ovipositor through the anal opening and deposits the egg in the posterior portion of the intestine. The majority of species of this genus stand upon the host when ovipositing.

A high degree of selectivity in oviposition is recorded for *Aphelinus semiflavus*, a solitary parasite of *Myzus persicae*. Only two or three instances of duplicate oviposition were detected by Hartley in 3,000 dissections. This selectivity persists even when parasitization approaches 100 per cent. The determination of prior parasitization is through exploratory thrusts of the ovipositor.

Little information is available regarding the reproductive capacity of members of the family. *Aphelinus mali* deposits a maximum of 140 eggs at the rate of approximately 9 each day. *A. semiflavus* produces an average of about 500 eggs under laboratory conditions, though the field deposition is estimated at only 200. The ovaries of gravid females

contain approximately 10 mature eggs, which indicates a daily deposition of about that number.

Larval Development.—None of the young larvae of the ectophagous species is capable of ordered movement, and consequently they maintain a permanent feeding position upon the host body. *Eretmocerus serius* has the unusual habit of being ectophagous during the first and a portion of the second stage (Fig. 65*D*), and it then enters the body of its aleyrodid host when the latter transforms to a pupa.

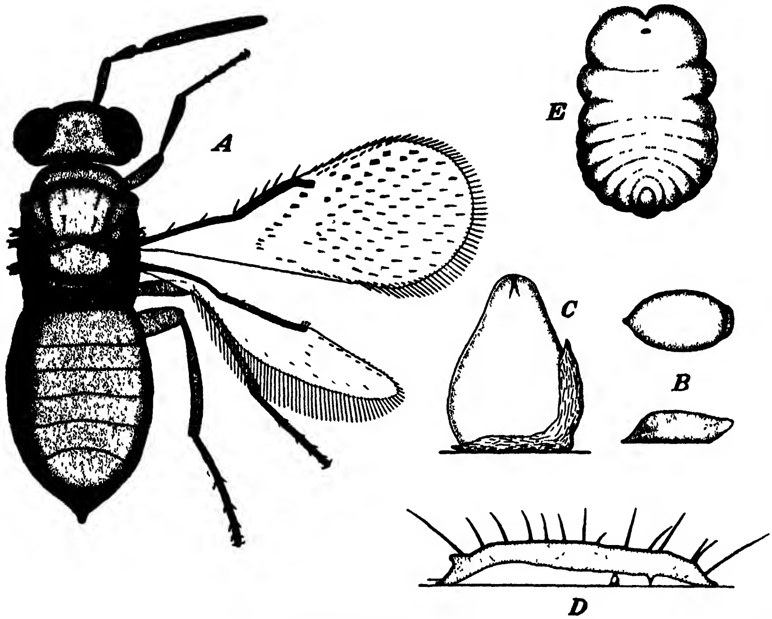


FIG. 65.—*A*, the adult female of *Eretmocerus serius* Silv.; *B*, the egg, dorsal and lateral views; *C*, the first-instar larva; *D*, host larva with first-instar *Eretmocerus* larva beneath the body; *E*, the mature larva. (*From Clausen and Berry*, 1932.)

Coccophagus ochraceus How., the single species of the genus known to be of ectophagous habit, is parasitic upon the immature females of *Saissetia*. Candaña has observed that the eggs are deposited upon the venter of the body, usually immediately behind the femur of one of the hind legs. During its first two stages, the larva feeds upon the body fluids through a puncture in the integument. Soon after the second molt, it makes a hole in the body wall of the scale just behind the proboscis, enters the body, and completes its development internally. There is thus a marked parallelism in habit between this species and *Eretmocerus*, the principal variation being in the time of entry into the host.

In *Casca parvipennis*, the rather elongate larva takes up a characteristically curved position in the body of *Aspidiotus* after its first molt,

and its body plane is always at right angles to that of the host. The eggshell and larval exuviae remain attached to the posterior end of the body. This occurs at times in *Physcus intermedia*, also.

In several species of *Aphytis*, which are normally ectophagous upon the females of diaspine Coccidae, the larvae are also predaceous upon the eggs. Numerous workers have dealt with this point in relation to *A. mytilaspidis*, but they are divided in their conclusions, several asserting that such feeding never takes place. In *A. chrysomphali*, the larva feeds upon the eggs if the body of the female scale is too shrunken, as a result of oviposition, to provide food of sufficient quantity and proper quality for the parasite.

A considerable number of species of *Coccophagus* attain the pupal or even the adult stage before death of the host takes place. In these instances, only a portion of the body fluids and the fat body have been consumed and the viscera remain intact. In order to pupate successfully, there must be some provision for meeting the respiratory requirements of the parasite during this period, and also for protection of the pupa. Timberlake (1913) mentions that *C. scutellaris* pupates within a protective shroud, presumed to be its unbroken last larval exuviae, which becomes filled with air. The same habit is found in *C. saintebeauvei* Gir. and among the females of *C. trifasciatus* Comp. and *C. capensis* Comp. Flanders (1938*a*) has made an extended study of this envelope and finds that, in the Aphelinidae as well as in other families, it is not a cast skin but a true cocoon, produced in film-like form rather than spun from a silken strand.

Taylor mentions that when several *Aspidiotiphagus citrinus agilior* develop in an *Aspidiotus* female the mature larvae are separated from each other by a delicate transparent septum. It is quite possible that this is of the same origin as the sheath of *Coccophagus*.

The adaptations for respiration have not been fully determined in the above species, but they are probably similar to those found in the Encyrtidae, particularly the genus *Encyrtus*, wherein a fusion takes place between the parasite cocoon and the tracheal system of the host. There are some indications that the older larvae of *E. serius* also derive their air supply from the tracheae of the aleyrodid host.

The orientation of the body of the parasite pupa with respect to its host is apparently dependent upon the form of the latter or, if it is a diaspine coccid, of its covering. The internal parasites consistently lie with the head at the posterior end of the host body, though in hosts that are nearly circular the position is irregular, and in *E. serius* the head is always at the anterior end. A rather peculiar feature in many species is the inverted position of the pupa, the venter being upward rather than turned toward the substratum. This occurs in *Aphelinus jucundus* and

A. semiflavus, parasites of aphids, and in *Eretmocerus*, *Aphytis chrysomphali*, *A. mytilaspidis*, and *Casca parvipennis*. This adaptation serves a definite purpose in those species having flattened bodies and contained in hosts that are broad and flat. In this position, the mouth parts of the newly transformed adult are already in contact with a free portion of the host body rather than that part which adheres to the substratum and through which emergence could not be effected. The shape of the body would prevent turning after the final molt. In *Coccophagus cowperi* Gir. and *Physcus intermedia*, however, the reverse position, with the venter downward, is taken.

Life Cycle.—The period of time required for development of the immature stages, from oviposition to emergence of the adult, is relatively short. *Marietta zebra* Kurd., a secondary parasite, requires only 12 days for its cycle, but the great majority of species reach maturity in 18 to 30 days at summer temperatures. *Aphytis chrysomphali*, which has a typical cycle, requires 3 days for incubation of the egg, 5 to 6 days for larval development, and 4 to 5 days for the pupal stage. *Aphelinus semiflavus* requires a longer period for development in large than in small aphids. In *A. mali*, a variation of as much as 20 days has been noted by Childs and Gillespie in the time of emergence of adults developing from eggs laid on the same day. Some species are able to oviposit the day of emergence, whereas others require a gestation period of 3 or 4 days. Flanders states that the species of *Coccophagus* are ready for oviposition the day following emergence.

The number of generations produced each year is exceedingly variable and is largely dependent upon availability of hosts in the proper stage for attack. *A. mali* has eight or nine generations each year upon the woolly apple aphid in some sections of the United States. *Aphytis chrysomphali* is stated to have only a single annual generation in Palestine, whereas in other subtropical and tropical regions having more favorable climatic conditions it may produce ten or more generations each year. When the host has several well-defined generations under field conditions, as is the case with many Aleyrodidae, the parasites are largely limited to a corresponding number. In contrast to this, *Coccophagus hawaiiensis* Timb., which attacks *Ceroplastes rubens* Mask. in Japan, has four generations to the single one of the host (Ishii, 1923).

Sex Ratio and Parthenogenesis.—Little information is available regarding sex ratios in the family. This situation is complicated by several factors, among which are the limitation of the two sexes to different stages of the same host or to entirely different hosts. Taylor points out that the two sexes of *C. parvipennis* rarely occur in the same batch of host scales, and progeny from small hosts are of the male sex.

Unisexual reproduction is normal in several species, among which are *Prospaltella berlesei* How., *Aphelinus jucundus*, and *A. semiflavus*.

Hartley secured only six males in 17 generations of the last species. Speyer (1927) states that *Encarsia formosa* produces a few males during periods of cool weather. Imms secured four males among more than 700 reared individuals of *Aphytis mytilaspidis*, and none was seen by Griswold in the course of extensive rearings.

Sex Differentiation in Host Relationships.—For many years, evidence has been accumulating pointing toward a differentiation in the relationships between the two sexes of aphelinid parasites and their hosts. In many families, it has been observed that females predominate from large hosts and males from those of smaller size, but this was considered to be due to the quantity of food available to the larvae. In the Aphelinidae, however, any explanation having a nutritional basis was inadequate to explain the various phenomena observed. Timberlake (1913) presented the first clear-cut evidence to give a genuine clue to the solution of the problem. Working with *Coccophagus lycimnia*, a primary internal parasite of the soft brown scale, *Coccus hesperidum* L., he found that females only were produced, generation after generation, upon that host. This species is commonly hyperparasitic upon *Microterys* and *Aphycus;* in such cases, strangely enough, it was found to be ectophagous in habit upon the mature larvae and pupae, and all progeny were males. Virtually identical observations were made by Taylor upon the reproductive habits of *Physcus intermedia* and *Casca parvipennis*, parasites of *Aspidiotus* and related genera in Java. Other authors have also recorded observations indicating, in various ways, departures from the normal habits of the family relating to reproduction. The accounts by Timberlake and Taylor contained the essential data required for a solution of the problem, but it was not until the admirable studies by Flanders (1936*a*, '37) upon *Coccophagus* that the real significance of their observations became apparent and an entirely new aspect of host-parasite relationships was revealed.

The genus *Coccophagus* is parasitic mainly in lecaniine Coccidae and in *Pseudococcus*, and includes many species of importance in the natural control of a number of major crop pests. They have consequently been imported into a number of countries, and particularly into California, in an attempt to control a series of destructive citrus pests of foreign origin. As these efforts went on, various unexpected difficulties arose. At times, attempts to rear species in pure culture resulted in repeated failure, whereas in others the progeny in some cases were males only or females only. This occurred in species that were known to reproduce bisexually.

Flanders's studies upon a series of species revealed an obligatory sex differentiation in host relationships whereby the females develop as primary parasites, without appreciable specialization, while the males develop only as hyperparasites. In the great majority of species, the

female larva is internal; yet the male in some is internal and in others external in habit. The grouping given below, adapted from Flanders, gives the range in the male sex, as compared with that of the females, in a series of species of *Coccophagus*, with examples of each habit.

A. Developmental habit of females.
- 1. Primary—all species of *Coccophagus*.
  - *a*. Ectoparasitic—*Coccophagus ochraceus* How.
  - *b*. Endoparasitic—all other known species.

B. Developmental habit of males.
- 1. Primary, identical with that of the female.
  - *a*. Ectoparasitic—*Coccophagus ochraceus* How.
  - *b*. Endoparasitic—*Coccophagus scutatus* How.
- 2. Indirect secondary.
  - *a*. Ectoparasitic—*Coccophagus trifasciatus* Comp.
  - *b*. Endoparasitic—*Coccophagus gurneyi* Comp.
- 3. Direct secondary.
  - *a*. Ectoparasitic—*Coccophagus lycimnia* Wlk.
Coccophagus heteropneusticus Comp.
Coccophagus malthusi Gir.
  - *b*. Endoparasitic—*Coccophagus scutellaris* Dalm.
Coccophagus capensis Comp.
Coccophagus rusti Comp.

A brief statement of the developmental habits of the males of a number of the above species will illustrate the great specialization that has occurred in this sex and the complexity of relationships as compared with those of the female.

In *C. gurneyi*, the egg is deposited in the body cavity of the mealybug host, and hatching is delayed until the body fluids have been consumed by a primary parasite. The young larva then attacks the mature primary larva, which may be of its own species, feeds externally for a short period, and then enters its body. The remainder of the first stage and all of the second are passed within this host, but shortly after the second molt it emerges and completes feeding externally. Upon *Leptomastix dactylopii* How., however, development is external in all larval stages. The above-mentioned delay in hatching until the body contents of the secondary host have been consumed clarifies the "inhibited" hatching observed but not understood by Cendaña, wherein eggs of *C. gurneyi* remained viable as long as 86 days but failed to hatch.

In *C. lycimnia*, the male egg is deposited externally upon the body of a mature primary larva or pupa in scale insects and mealybugs. Larval development is entirely external.

The male egg of *C. scutellaris* is deposited in the body cavity of the larva of a young primary parasite, preferably of its own species. Larval development is entirely internal, but the larva leaves the body of the primary for pupation, which takes place within the shroud or sheath of

the latter. Development of *C. capensis* is identical except that the prepupa and pupa are initially attacked.

The marked differences in the developmental habits of the immature stages is correlated with a sexual dimorphism in the first- and second-instar larvae and, in some species, in the deposited eggs as well. These will be discussed in the following section.

The existence of sex differentiation in host relationships is, of necessity, accompanied in several species by a marked difference in the oviposition responses of virgin as compared with mated females. The unmated females have the instincts of hyperparasites and are attracted only to previously parasitized hosts, whereas after mating they are attracted to and oviposit in the body cavity of unparasitized hosts. *C. trifasciatus* and *C. gurneyi*, the male larvae of which are indirect secondary parasites, show no differences in this respect between mated and unmated females.

These discoveries not only solve various previously unexplained phenomena in *Coccophagus* but also provide a probable explanation of diverse occurrences in other genera of the family. Tower (1914) found that young larvae of *Prospaltella perniciosi* Tower were often contained within the bodies of older larvae of the same species, and Rice (1937) has since determined that the male develops only as an indirect internal parasite of the female larva.

In their attempt to introduce *P. divergens* Silv. from Malaya into Cuba, Clausen and Berry experienced difficulties that may have been due to a somewhat similar habit. A shipment of this parasite in Wardian cases stocked with *Aleurocanthus woglumi* produced several generations en route and, upon arrival, yielded approximately one thousand adult females. As no males appeared, it was assumed that the species reproduced unisexually. A portion of the above number was liberated in the field, some were liberated upon infested plants in an insectary, and others upon infested plants enclosed in cellophane bags. Not a single individual was reared from this large number, and the stock was consequently lost. No satisfactory explanation of this outcome could be found at the time, and it remained a mystery until the discovery of sex differentiation in host relationships. It was then recalled that the shipment inadvertently contained a small number of *Eretmocerus serius*, which may have been the host of a sufficient number of males to maintain the stock en route.

Taylor's observations on parasites of *Aspidiotus* in Java point strongly toward a differentiation in host relationships in *Physcus* and *Casca*. *P. intermedia* was noted frequently to parasitize mature larvae and pupae of its own species, though not of other species in the same host, and all individuals developing in this way proved to be males.

For *C. parvipennis*, the evidence is not so complete. It has been reared as an internal parasite of the mature larvae and pupae of its own species, and of *Comperiella*, and these individuals were invariably males. It is stated, however, that the progeny reared as primary parasites from early second-instar *Aspidiotus* were of both sexes.

Knowledge that this type of reproduction is of common occurrence, at least in the Aphelinidae, is of great importance in the practice of biological control. It demonstrates the need of studying the oviposition behavior of both the unmated and the mated females and likewise of a detailed examination, by dissection of hosts containing the different immature stages, to determine the exact host relationship of each sex. It is only by such a thorough study that suitable conditions can be provided for successful insectary rearing or field colonization.

EFFECT OF PARASITISM UPON THE HOST

The species of the family that attack Aleyrodidae complete their development and emerge from the host pupa, so that any reproduction by parasitized individuals is impossible. In the case of the aphid hosts of *Aphelinus*, the effect varies with the parasite species and with the stage of development of the host at the time of attack. Many of the nymphs of *Macrosiphum cornelli* Patch attacked by *A. jucundus* Gahan are permanently paralyzed and the younger individuals are almost invariably killed, whereas those which are destined to bring the parasite to maturity are only temporarily paralyzed. The mature individuals of *Eriosoma lanigerum* Hausm., attacked by *A. mali*, continue to produce young during a period of seven or eight days following oviposition by the parasite. In *Myzus persicae* Sulz., the newly hatched nymphs attacked by *A. semiflavus* never reach maturity, whereas if adults are attacked the production of young is continued for about six days.

The species that are external parasites of diaspine scales seem to prevent the further development of the host after it is attacked. In the case of adult females of *Aspidiotus destructor* parasitized by *Aphytis chrysomphali*, oviposition ceases at the time the parasite egg hatches. The same is true of *A. mytilaspidis* on *Lepidosaphes ulmi* L. *A. chrysomphali*, which attacks the early stages of *Aonidiella aurantii* Coq., is said to prevent further development, and no molts occur after parasitization. *Physcus intermedia* attacks the early third instar of *Aspidiotus destructor*, and oviposition is completely prevented.

Information on the effect of parasitism upon reproduction of lecaniine Coccidae is available only for those attacked by several species of *Coccophagus*. The majority of species of this genus attack the early instars of the host, and death occurs before maturity is reached, though not until the parasite itself is in an advanced stage of development. *Sais-*

setia oleae Bern., the host of *C. saintebeauvei*, is still alive at the time of emergence of the adult parasite, whereas it survives only until the pupation of *C. capensis*. All species kill their hosts before reproduction can take place.

Many species of *Coccophagus* that develop in the early stages of lecaniine Coccidae produce a characteristic blackening of the host integument. This has been noted in *C. cowperi* and *C. lycimnia* but is lacking in *C. scutellaris*. A similar coloring is also conspicuous in *Trialeurodes* parasitized by *Encarsia formosa*.

IMMATURE STAGES

The ovarian eggs of many species of the family that have been observed are of the two-bodied type such as is found in several other families. At deposition the contents are forced into the main body, and the "bulb" remains as a more or less collapsed stalk or hook. This form of egg is common to *Aphytis*, *Centrodera*, and *Aspidiotiphagus*. In *Marietta zebra* and others, the laid egg (Fig. 66*D*) is much like the ovarian form except that the anterior stalk is appreciably reduced in size. This species is distinguished from others of the family by having the chorion of the main body covered with small papillae.

The eggs of *Ablerus*, *Casca*, *Encarsia*, *Eretmocerus*, and *Physcus*, and those of *Coccophagus* of primary habit, are of simple form, ranging from lemon-shaped to kidney-shaped and cylindrical. That of *Eretmocerus serius* (Fig. 65*B*) is distinctly flattened, owing presumably to its being compressed between the host body and the leaf after deposition.

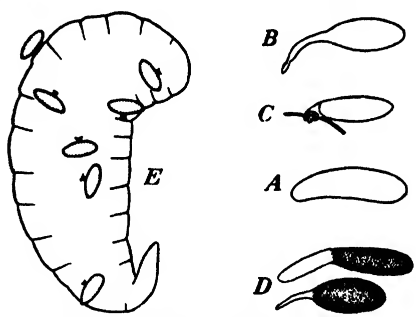


FIG. 66.—Eggs of the Aphelinidae. *A*, ovarian and laid female egg of *Coccophagus heteropneusticus* Comp.; *B* and *C*, the laid male egg of the same, the latter after the insertion of the anterior end into a puncture in the host skin (*from Flanders*); *D*, ovarian (above) and laid egg of *Marietta zebra* Kurd. (*from Silvestri*, 1919); *E*, eggs of *Euxanthellus philippiae* Silv., probably male, upon a mature larva of *Coccophagus* (*from Smith and Compere*, 1928).

Smith and Compere record an unusual modification in the egg of *Euxanthellus philippiae* Silv. The ovarian egg is simple; yet after its deposition it is found to be attached to the host larva by a pedicel arising at the center of the ventral side (Fig. 66*E*). This pedicel apparently is formed in the same manner as that of the male eggs of *Coccophagus lycimnia* and *C. heteropneusticus* Comp., which are discussed in the following section, and it may, in fact, be a male egg, also.

The first-instar larvae of the species that show no sexual dimorphism are of two types, the hymenopteriform and the caudate. The hymenopteriform larvae range from elongate to almost spherical in form and bear no appendages or integumentary setae. To this group belong the larvae of *Aphelinus*, *Eretmocerus*, *Prospaltella*, *Aphytis*, and *Aspidiotiphagus*. The larva of *E. serius* (Fig. 65*C*) is pear-shaped and shows no evidence of segmentation. Those of endophagous habit usually have only a simple internal tracheal system and no spiracles. Among the species that develop externally the number of spiracles is variable, ranging from five in *M. zebra* to eight in *Aphytis mytilaspidis* and *A. longiclavae* Mercet, though none was detected in *Eretmocerus*.

The caudate larva is not encountered frequently in this family, though it has been described for *Aspidiotiphagus citrinus.*

It is often difficult to determine the number of instars because of the minute size of the larvae and the lack of heavily sclerotized parts which might distinguish the successive exuviae. There are apparently only three, in contrast to the five found in several related families. The second and third instars possess no distinctive features and need not be described. The mature larvae usually have nine pairs of spiracles, though *Coccophagus hawaiiensis* and *Aphelinus semiflavus* are said to have only five.

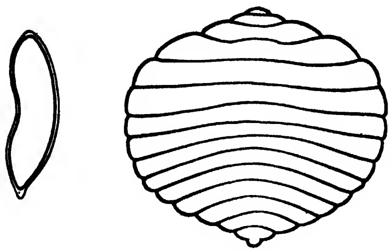


Fig. 67.—The egg and mature larva of *Aphelinus mali* Hald. (*From Lundie,* 1924.)

The pupae of a number of genera that attack diaspine Coccidae are conspicuous because of the extreme compression in the dorsoventral plane. In some species of *Aphytis,* the thickness is only one-fourth the width of the body. The pupa of *Physcus intermedia* has an exceptionally heavily sclerotized integument, black in color and similar to that found in various Eulophidae.

Sexual Dimorphism in the Immature Stages of Coccophagus.—In the species of this genus that develop, in both sexes, as primary parasites, there is no departure from the normal of the family in the egg or larval forms, those of the two sexes being identical. Sex differentiation in host relationships in a group of species has involved a specialization in habits of the male that is reflected in several modifications in form to meet more successfully the conditions encountered. Flanders has described and figured the female and male eggs and early larval instars of several species.

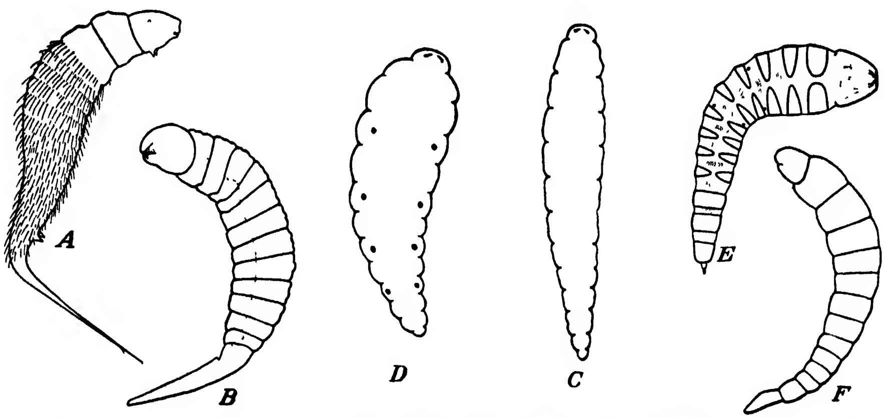


Fig. 68.—Sexual dimorphism in the first-instar larvae of *Coccophagus.* *A* and *B*, male and female larvae of *C. capensis* Comp.; *C* and *D*, male and female larvae of *C. heteropneusticus* Comp.; *E* and *F*, male and female larvae of *C. gurneyi* Comp. (*After Flanders.*)

The ovarian and laid female eggs of *C. lycimnia* and *C. heteropneusticus* (Fig. 66*A*) are somewhat cylindrical, though slightly broader at one end, slightly curved, and smoothly rounded at both ends. The male egg (Fig. 66*B*, *C*), on the other hand, is drawn out at the anterior end into an irregular stalk-like process which, at deposition, is twisted into a button-like pedicel when it is inserted into a puncture in the host integument.

The first-instar female larva of *C. capensis* (Fig. 68*B*) is of the caudate type, whereas the male (Fig. 68*A*) is of a distinctive form, having the segments clothed in long setae and the last abdominal segment extended into a long, spine-like process. Both sexes have only an internal tracheal system. The male larva of *C. scutellaris* is of similar form.

The first-instar female larva of *C. heteropneusticus* (Fig. 68*D*) is rather elongate and lacks an open tracheal system, whereas the male (Fig. 68*C*) is more robust and has spiracles on the last thoracic and the second, fourth, and sixth abdominal segments.

C. gurneyi has a first-instar larva female (Fig. 68*F*) that is slender, tapering posteriorly, and has only an internal tracheal system. The male (Fig. 68*E*) is of a modified planidium type, with heavily sclerotized segmental plates and two pairs of spiracles, situated on the intersegmental membrane just in front of the third and fifth bands, representing the first and third abdominal segments.

The ectophagous male larva of *C. lycimnia* is robust in form, with spiracles on the metathorax and on the second, fourth, and sixth abdominal segments.

ENCYRTIDAE

The members of this family are most frequently found attacking the homopterous family Coccidae, especially the Lecaniinae and Dactylopiinae, though other families such as the Aphididae and Cercopidae also serve as hosts. In the hemipterous family Pentatomidae and in closely related forms, only the egg stage is attacked. Many Lepidoptera are parasitized, some by species that develop in the eggs and others in the larvae. In this latter group are several genera that are capable of polyembryonic reproduction, it being possible that several thousand individuals may emerge from a single host. Among the Coleoptera, the larval and pupal stages of the Coccinellidae and Chrysomelidae most frequently serve as hosts. Dipterous pupae, particularly those of the Syrphidae and Cecidomyiidae, are often parasitized. Several species are recorded from neuropterous cocoons, principally of the genus *Chrysopa*. Occasional, instances are known of attack upon other orders and families in addition to those mentioned. Finally there are the internal parasites of the nymphs of ticks (Ixodidae), represented by the genera *Hunterellus* and *Ixodiphagus*.

In the role of secondary parasites, we find representatives of the family developing in Coccidae and Aphididae and in lepidopterous eggs, the primary hosts being the immature stages of other Chalcidoidea, etc. Several genera are known to parasitize the immature stages of the Dryinidae in their cocoons.

A considerable number of species of the family have been utilized in the biological control of crop pests, particularly of the scale insects. The following species have adequately controlled their respective hosts in one or more countries:

Species	Host
Anagyrus dactylopii How.	*Pseudococcus filamentosus* Ckll.
Blastothrix sericea Dalm.	*Eulecanium coryli* L.

Species	Host
Habrolepis dalmani Westw.	*Asterolecanium variolosum* Ratz.
Pseudaphycus utilis Timb.	*Pseudococcus nipae* Mask.

In addition, several other species have been responsible for an appreciable reduction in the host populations, though not sufficient to eliminate entirely the need for other control measures.

BIOLOGY AND HABITS

With exceedingly few exceptions the members of this family develop as internal parasites, the only exceptions being the occasional species of *Microterys* which are predaceous upon the eggs of Coccidae. This habit was observed by Silvestri (1919*b*) in the case of *M. sylvius* Dalm. in

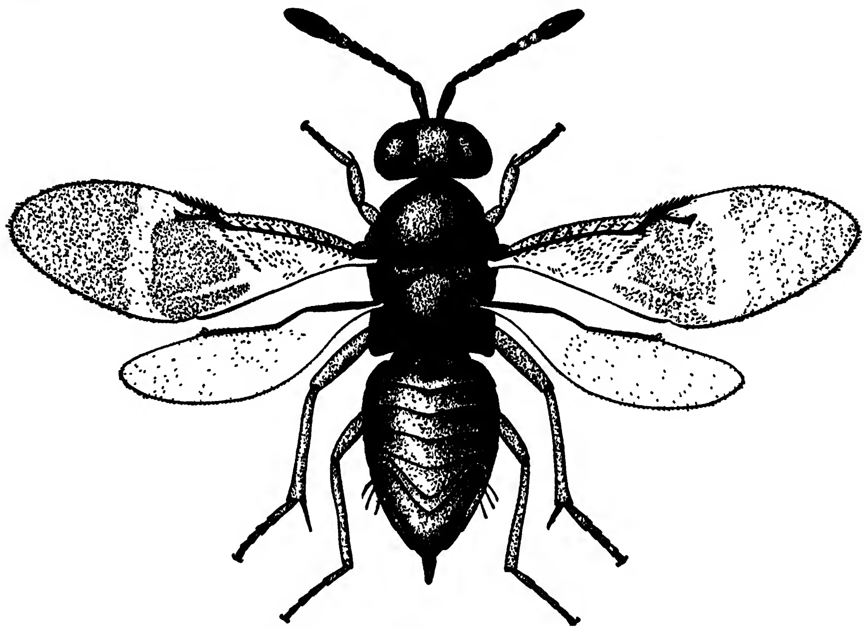


Fig. 69.—The adult female of *Microterys clauseni* Comp. (*Original.*)

relation to *Eulecanium coryli* L. in Italy. The record was not based upon a complete study of the species and was regarded with considerable doubt until the recent discovery of another species of the genus, *M. titiani* Gir., having the same habit (De Bach, 1939).

The hyperparasitic species are usually direct in their relationship, though *A. aphidivorus* Mayr is an indirect secondary parasite of *Macrosiphum cornelli* Patch through *Aphelinus jucundus* Gahan (Griswold, 1929).

Habits of the Adult.—In general, the adult females of this family contain fully developed eggs at the time of emergence, and they are consequently able to oviposit immediately. Among certain of the multi-

brooded species that are parasitic in single-brooded Coccidae, there is, however, a period of diapause at the beginning of adult life of the females of the summer brood that may be of advantage to the parasite during the period when the host is not in a suitable stage of development for parasitization. Silvestri (1919*a*) observed that the second brood of adults of *Blastothrix sericea* refused to oviposit in young host scales, and an examination of their ovaries showed them to be much reduced during the summer and early autumn. Reproductive activity apparently is revived during the autumn, for first-instar larvae were found in second-instar hosts in November.

The species that attack Homoptera derive their food largely from the honeydew secretions of their hosts, though a number feed directly upon the body fluids of the host. Several species of *Ooencyrtus* feed at punctures made in the host egg in which their progeny are to develop.

The activities of the parasite female incident to host examination, feeding, and oviposition are particularly well-illustrated in *Microterys clauseni* Comp. parasitic in *Ceroplastes floridensis* Comst. in Japan. The preliminary activities are sharply distinguished from insertion of the ovipositor for oviposition. The female first examines the host scale carefully with the antennae; after this, she mounts upon its dorsum; and, after a further slight examination in that position, she then inserts the ovipositor perpendicularly into the body. This insertion and the probing that follows are not for oviposition but may serve two purposes; to determine whether the host is in a suitable physical condition and whether it is already parasitized. At times, feeding takes place upon the fluids that exude from the wound. When the examination is complete and the host proves to be satisfactory, the female dismounts from the dorsum of the scale, approaches the caudal end of the body, and inserts the ovipositor, by a backward thrust, between the anal plates. The egg is deposited in the intestine and lies with the anterior portion of the stalk extruded between the plates (Fig. 73*D*). This placement of the egg is constant and has been recorded also for *Eusemion corniger* Wlk. (Martelli, 1910) and *Diversinervus elegans* Silv. (Compere, 1931).

Metaphycus lounsburyi How. has the unusual habit of inserting the ovipositor beneath the margin of the body of the half-grown *Saissetia* female and piercing the body wall from beneath. With the exceptions noted above, the species attacking Coccidae insert the ovipositor through the dorsum.

The oviposition habit of the hyperparasitic *Aphidencyrtus aphidivorus* is distinctive in that the female stands upon the dorsum of the living aphid, inserts the ovipositor perpendicularly, and probes about until the young *Aphelinus* larva is located, whereupon its body is pierced in turn and the egg is then deposited. Rather surprisingly, the aphid

host appears not to be inconvenienced or to suffer any discomfort during this act; it may possibly be already sluggish as a result of the activities of the *Aphelinus* larva within its body.

Feeding by the adult females upon the body fluids of the host usually does not result in serious injury to the latter. In several other families, it is known that certain species which oviposit in the host egg or whose larvae are egg predators completely consume the contents of the eggs upon which they feed, and this habit is possibly of greater importance in reducing the host population than is the parasitic or predaceous habit of the larvae. Maple's (1937) recent observations on *Ooencyrtus johnsoni* How. indicate that its stinging of the eggs of *Murgantia histrionica* Hahn incident to feeding may likewise result in a heavy mortality. He found that a very large majority of eggs that had been punctured with the ovipositor failed to hatch, even though oviposition did not take place. The death of the embryo is due not to the abstraction of appreciable quantities of fluids from the egg but probably either to mechanical injury or to the injection of some toxic agent at the time of stinging.

Relatively little is known regarding the reproductive potentials of the monembryonic members of the family. The maximum recorded is approximately 250 for *Microterys speciosus* Ishii, and the majority of species probably do not deposit greatly in excess of 100 to 150 eggs. Ishii found an average of 172 mature eggs in the ovaries of gravid females of *Aphycus timberlakei* Ishii. Crossman (1925) states that virgin females of *Ooencyrtus kuvanae* How. deposit a much smaller number of eggs than do those which are mated. Maple found that mating had no influence upon the oviposition activities of the females of *O. johnsoni;* in fact, one unmated individual produced 224 male progeny, a number considerably in excess of that secured from the mated females. The oviposition period of this species covers approximately three weeks.

Egg and Larval Development.—In a number of instances, it has been observed that a marked increase in size takes place among the stalked eggs during the course of incubation. The dimensions given by Clancy for the egg of *Chrysopophagus compressicornis* Ashm. are 0.16 by 0.06 mm. for the egg body at the time of deposition and 0.73 by 0.27 mm. on the fourth day, immediately before hatching. This is exceeded in *Tetracnemus pretiosus* Timb., the egg of which increases in length from 0.03 or 0.04 mm. to 0.25 mm. In *Chrysopophagus*, the trophic membrane is seen, completely enveloping the embryo, one to two days after deposition. Through this membrane, food materials are derived from the body fluids of the host. It envelops the body of the first-instar larva throughout the stage, allowing the head and tail to protrude.

The functioning of the distinctive longitudinal rib or plate on the encyrtiform egg of *Microterys* and many other genera has been the sub-

ject of speculation for many years. It had been generally assumed that the egg stalk, which protrudes through the integument of the host, serves as a tube through which the larva draws its air supply from the outside. Timberlake (1913) states that the larva "maintains, without the least doubt an intimate and vital connection with the egg stalk, and the latter might properly be called a living part of the organism." The above explanation, however, ignores the relationships of the rib to this function.

The first observations relating to the manner of respiration of the larva through an egg of this type, in which the distinctive rib was described in detail and considered from the point of view of its function, were by Silvestri (1919) upon a series of species parasitic in lecaniine Coccidae in Italy. He noted that the interstices of the "cells" of the rib were filled with air and hence designated the structure as the "aeroscopic plate" but concluded that actual respiration of the larva is through the lumen of the tube itself. The plug at the outer end of the stalk was believed to be permeable to gases, and exchange was thought to be accomplished by diffusion.

More recently, the structure and manner of functioning of this plate, as it occurs in *O. johnsoni*, have been the subject of study by Maple (1937). His observations have revealed that the single pair of caudal spiracles of the larva are always in direct contact with the plate of the egg body and that the location of this point of attachment has no relation to the egg stalk. No aperture could be found in the external plug of the egg by means of which air can pass through the lumen of the stalk. Tests with various stained oils indicated ready penetration of the interstices of the plate and thence into the tracheal system of the larva. No penetration into the lumen of the stalk was secured. These experiments demonstrate that the aeroscopic plate, rather than the lumen of the stalk, provides the channel through which the outside air reaches the spiracles of the parasite larva within the body of the host.

It is not yet clearly understood how the air supply contained in the interstices of the rib reaches the spiracles of the larva. The rib is external whereas the posterior end of the larva, bearing the spiracles, remains within the cup-like egg shell. Either the chorion beneath the plate must be permeable, or perforations are made in some way by the larva so that the air supply in the plate becomes accessible.

It had been assumed that all eggs of this type which project through the integument of the host and to which the larvae are affixed possess the aeroscopic plate. Clancy has found, however, that the egg of *Isodromus iceryae* How. lacks the plate and that the shell and stalk have no function other than to hold the young larva in position. Silvestri had previously mentioned that the first-instar larva of *Aphycus melano-*

stomatus Timb. (*A. punctipes* Dalm.) lacked the caudal spiracles even though arising from an encyrtiform egg but still believed that the air supply was derived through the egg stalk.

In all the accounts of development of encyrtiform eggs and larvae, it has been pointed out that the posterior end of the larva is encased in the eggshell, but no mention is made regarding the manner in which that position is attained. The stalk is at the anterior end of the egg, and the head of the embryo would therefore be formed near the base of the stalk and the posterior end of the body, bearing the spiracles, at the opposite end. In Maple's illustration of the mature embryo of *O. johnsoni* within the egg, the opposite orientation is shown, with the posterior end of the body at the anterior end of the egg and the spiracles in contact with the aeroscopic plate at the base of the stalk. His illustration of the newly hatched larva of *Anagyrus yuccae* Coq., however, indicates a normal orientation prior to hatching.

It is evident that the position of the young larva with respect to the eggshell is brought about either by a rotation of the developing embryo within the egg or by a reversal of position of the larva immediately after hatching. The former appears to be true in *O. johnsoni*, and observations upon *Microterys clauseni* indicate a similar movement prior to hatching.

Larvae of the encyrtiform type usually maintain their connection with the egg stalk until the final larval stage and utilize it for respiration during this entire period. The successive exuviae are forced back over the body and become a part of the sheath enveloping the posterior end of the body. A count of these exuviae consequently establishes definitely the instar of a larva of this type.

The encyrtiform larva of *M. clauseni*, which is found in the hind intestine of *Ceroplastes*, apparently limits its feeding to the contents of the digestive tube, and it is only after the second molt that the intestinal wall is broken and direct feeding upon the viscera and body fluids takes place. Death of the host usually occurs 10 to 12 days after parasite oviposition.

In a considerable number of species that have stalked eggs, it has been noted that a varying proportion of individuals may also retain the eggshell and the cast skins as an envelope about the caudal end of the body (Fig. 75). This habit is associated with larvae of both the hymenopteriform and the caudate types, which are free-living in the host body, and serves no apparent purpose. In *C. compressicornis*, the successive exuviae cover a considerable portion of the body, and the mandibles of the first two can be readily distinguished on the mid-ventral area of the third-instar larva.

The number of larval instars in the Encyrtidae is variable and ranges from two to five. *Anarhopus sydneyensis* Timb. is the single species

stated to have only two (Compere and Flanders, 1934); this was determined by clearing and staining parasitized mealybugs containing full-grown larvae. Indications of only one cast skin were found. The greater number of species that have been studied are said to have three instars, though several have four or five. It is probable, however, that the great majority have five and that the lesser number recorded in many instances is due to the early exuviae having been overlooked. The exact number can usually be determined only by clearing and staining the entire host contents; by this means the mandibles, at least, become recognizable and can be measured.

The most striking modifications in larval development of the Encyrtidae relate to respiration of encyrtiform larvae during the later stages; at this time, a functional relationship is established by some species with the tracheal system of the host. This phenomenon has been demonstrated to exist in *Encyrtus infelix* Embl. (Embleton, 1904; Thorpe, 1936), *E. infidus* Rossi (Clausen, 1932*b*), *Aphycus melanostomatus* Timb. (Imms, 1918), and *Carabunia myersi* Waterst. (Myers, 1930). *Carabunia* is parasitic in the nymphs of the froghopper, *Clastoptera undulata* Uhler, and the remaining species attack lecaniine Coccidae. All these, with the possible exception of *A. melanostomatus*, pupate and emerge while the host is still alive. The course of events may be briefly stated as follows: When approaching maturity, but before the last molt, the parasite larva becomes invested with a membranous sheath. At approximately the same time, the tracheal branches of the host fuse with, or become attached to it, in the immediate vicinity of each of the four parasite spiracles. At this time, the functional connection of the larva with the egg stalk is broken. The sheath, which surrounds the larva and later the pupa (Fig. 70*D*), becomes filled with air, and the oxygen supply of the parasite is derived therefrom. Miss Embleton, who was first to observe this remarkable adaptation, surmised that the sheath was probably a cast larval skin, and this interpretation was followed by several later authors. Imms concluded that it arises as a chitinous proliferation of the host tracheae, whereas Thorpe, after a detailed study, has recently stated that it is of host origin but produced by phagocytic action, in the building up of which the fine tracheal branches play a part.

More recently, Flanders (1938*a*) has arrived at what appears to be the correct conclusion as to the origin of this sheath. He found that the ileac and labial glands of the larvae are apparently identical in function and that they produce a viscid material which exudes from both ends of the body and spreads to form a thin protective covering. The sheath of *Encyrtus* is consequently a cocoon, in film form rather than composed of strands, and is identical in origin with the common spun cocoon. The sheaths enveloping the larvae and pupae of other endoparasitic

Chalcidoidea, particularly the Encyrtidae and Aphelinidae, are developed in the same way.

Although Thorpe's interpretation of the origin of the sheath of *E. infelix* apparently is not valid, yet his explanation of the manner in which the connections between the sheath and the host tracheae are brought

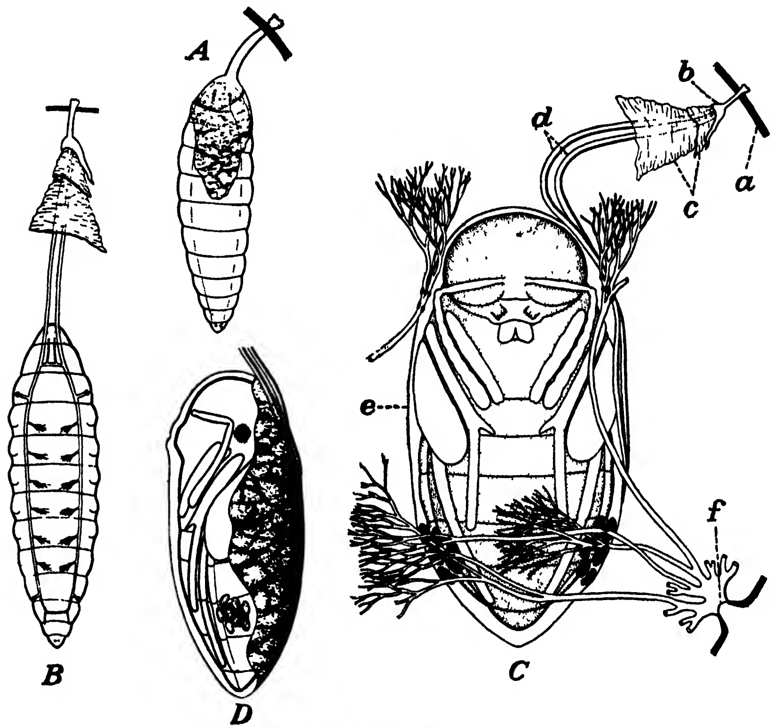


FIG. 70.—Immature stages of *Encyrtus infidus* Rossi. *A*, the first-instar larva, showing the eggshell enveloping the posterior segments; *B*, the third-instar larva, showing the long caudal spiracular stalks, with the spiracles fixed in the cup-like exuviae of the preceding instars; *C*, a ventral view of the pupa within the sheath, showing connections with the tracheal system of the host; *D*, a lateral view of the pupa within the sheath, showing the darkened larval exuviae upon the dorsum and the meconial pellets grouped at the posterior spiracular area. (*From Clausen*, 1932.)

about is of particular interest. As the sheath develops, the adjacent tracheal trunks of the host form a union with it in the immediate vicinity of the larval spiracles. This is stated to be the result of a physiological rather than a mechanical reaction. The tracheal epithelium is activated by a sudden change in respiratory activity, such as a lowering of the oxygen tension or an increase in carbon dioxide concentration incident to the approach of the pupal stage and to the stoppage of an adequate air supply through the egg stalk. Such a stimulus would naturally be most strongly felt in the areas surrounding the open spiracles. The

sharp bending of the tracheal branch, which is evident at the point of attachment, results in most cases, if not in all, in a definite fracture of the tracheal lining.

Another interesting feature in the biology of *Encyrtus* is the habit of the mature larva of reversing its position within the sheath prior to pupation. This occurs whether the parasite is solitary in young scales, as *E. infelix* in *Saissetia hemisphaerica* Targ., or gregarious, as *E. infidus* in *Lecanium kunoensis* Kuw. In the latter case, an average of 6.4 *Encyrtus* individuals reach maturity in each full-grown female scale. Without a reversal in position, the pupae and the newly transformed adults would lie with their heads directed downward toward the venter of the scale, and emergence from the living host would be difficult. As it occurs, however, the head of the pupa is directed outward near the point of insertion of the egg, and the instincts of the adult to move directly forward bring it quickly to the body wall of the host where emergence is soon accomplished.

The reason for the change in position in *E. infelix* is not nearly so apparent; for the solitary parasite is oriented along the longitudinal axis of the host, and emergence of the adult would presumably be as readily accomplished from one end as the other. According to Thorpe, "That this turning movement is the result of an innate instinct and is not dependent on some stimulus provided by the tissues of the host is shown by the fact that even in those rare cases where the egg has been deposited anteriorly the tendency to turn is still manifest."

So far as respiration by the pupa is concerned, the change in position has little effect, for in either case the two points of fusion of the sheath and the host tracheae would overlie the two pairs of functional spiracles of the pupa.

The manner of formation of the sheath, and the pupation habit of *Carabunia myersi* are apparently identical with those of *Encyrtus*, but it is noteworthy that the early larval instars are of the caudate type rather than encyrtiform. Tracheal attachment may occur at several or all of the six larval spiracles. The sheath does not become filled with air until sometime after pupation, whereas in *Encyrtus* the connection is functional during the last larval stage and air bubbles surround the pupa at its formation.

The solitary encyrtid parasites of mealybugs produce a pronounced inflation of the host body, causing it to become circular in cross section, cylindrical, and smoothly rounded at both ends. The interior of the shell is smooth and often highly polished, as if by a secretion provided by the parasite itself. These parasitized mealybugs are commonly referred to as "mummies" and bear a marked superficial resemblance to certain dipterous puparia. The gregarious species, such as *Acerophagus*

notativentris Gir., produce a similar inflated condition, and each of the surface cells is distinctly outlined externally.

In certain species of hyperparasitic habit, pupation takes place within the larval skin of the primary host. This is illustrated by *Quaylea whittieri* Gir., a solitary internal parasite of the mature larvae of *Scutellista, Metaphycus,* and other parasites and egg predators of *Saissetia* and related Coccidae. The larval skin of the host parasites becomes much distended and darkened, and here, also, the resemblance to dipterous puparia is noticeable.

The effect of the stage of host development at the time of attack upon the cycle of the parasite is strikingly shown in the case of *Hunterellus hookeri* How. (*Ixodiphagus caucurtei* Buy.) (Cooley, 1928; Cooley and Kohls, 1933; Brumpt, 1930), which develops internally in many species of ticks in various parts of the world. The eggs are deposited in the nymphal instars of the host, and development of the larvae is delayed until the host has become engorged with blood. This has been termed "latent parasitism," and under some conditions a period of six months may elapse from the time of oviposition until the host shows evidence of parasitization. This obligatory diapause in the early larval stage is imposed by the host and is apparently due to the nutritional requirements of the parasite larva not being met until the host has become fully fed.

Sex Ratio and Parthenogenesis.—The great majority of the Encyrtidae reproduce bisexually, and there is usually a slight preponderance of females among the progeny, the extreme in this respect being a ratio of 5.3 to 1 in *Zarhopalus sheldoni* Gir. (Clausen, 1924). An apparent exception to this rule is found in *Tetracnemus pretiosus* in which the males are in excess in the ratio of 1.4 to 1 (Clancy, 1934). This record is based on laboratory rearings and may differ from the normal field ratio. The field ratio of *Ooencyrtus johnsoni* is approximately 4 to 1.

A marked difference is found in the sex ratios of the overwintering and spring generations of *Microterys clauseni* in *Ceroplastes.* The first generation is solitary in young scales, and the adults that emerge in the early spring are predominantly female, in the ratio of 3 to 1. In the second generation, which is gregarious in the mature scales, an average of 3.15 individuals develop in each scale, and the ratio is increased to 9 to 1. Parthenogenetic reproduction results in male progeny only. The peculiar feature about the reproductive habits of this species is that the "brood" in each scale consists of one sex only. In a series of 73 *Ceroplastes* females isolated individually for parasite emergence, not a single exception to this rule was found. The explanation of this phenomenon is not clear; for the eggs are deposited singly, and the females

show no hesitation in ovipositing in hosts that already contain one or more eggs. Thus the parasite content of a scale is frequently the result of successive ovipositions by several females over a period of days.

Unisexual reproduction is normal in a number of species. Embleton secured only a single male among 1,000 adults of *Encyrtus infelix*, and only a single one has been secured among the extensive rearings of the same species in Hawaii. Timberlake (1919) records the same reproduction habit in *Adelencyrtus odonaspidis* Full., *Blepyrus mexicanus* How., *Pauridia peregrina* Timb., and *Saronotum americanum* Perk. To this list may be added *Anagyrus subalbicornis* Gir., *Habrolepis dalmani*, and *Comperiella unifasciata*. Occasional males have been reared in most of these species, but they apparently play no part in normal reproduction. As opposed to this conclusion, it is stated by Ishii that virgin females of *Microterys speciosus* produce only female progeny, whereas those which are mated produce both sexes. Parker and Thompson (1928) mention that their rearings of the polyembryonic *Copidosoma thompsoni* Mercet have not yielded a single male, though they do not state that reproduction is unisexual.

Polyembryonic Reproduction.—Among the Chalcidoidea, the Encyrtidae is the only family at present known to contain representatives exhibiting the polyembryonic mode of reproduction. This is confined, so far as has been conclusively demonstrated, to a group of closely related genera comprising *Ageniaspis*, *Litomastix*, *Paralitomastix*, and *Copidosoma*. The evidence indicates that most, if not all, species of these genera probably reproduce in this way. The known hosts are, without exception, the larvae of Lepidoptera.

The more comprehensive contributions on polyembryonic reproduction in the family are those by Marchal (1898, 1904) on *A. fuscicollis* Dalm. and *A. testaceipes* Ratz.; Silvestri (1906, '08, '14*a*) on *L. truncatellus* Dalm., *A. fuscicollis praysincola* Silv., *C. buyssoni* Mayr., *C. tortricis* Waterst., and *C. nanellae* Silv.; Martin (1914) on *A. fuscicollis;* Patterson (1915, '17, '18, '21*a*) on *C. gelechiae* How. and *L. floridanus* Ashm.; Leiby (1922) on *C. gelechiae;* and Ferriere (1926*b*) on *L. kriechbaumeri* Mayr.

Bugnion (1891) was first to observe the presence of embryo "chains" of *A. fuscicollis* Dalm. in the larvae of *Hyponomeuta*, but he did not attribute them to polyembryonic development, a phenomenon not known at that time to occur among the insects. It was not until the publication of the classic series of papers by Marchal, the first of which appeared in 1898 and which dealt not only with *Ageniaspis* but also with several platygasterid genera of similar habit, that the true explanation of their origin was revealed.

There is a marked degree of uniformity in habit among the members of this group. All deposit the egg within the embryo of the host egg, and the host attains the mature larval stage before death. In some species, a few host individuals may reach the pupal stage. At the time the parasite larvae attain maturity, the body of the host becomes much distended; it is often twice or more the size of a healthy larva. It is frequently considerably distorted, with a mummified appearance (Fig. 71), and the uneven surface shows each of the outer parasite pupation cells distinctly. In other species, the bodies are distended but not deformed. The number of parasites that are able to complete development in a single host is, of course, dependent upon the size of the latter The species that are definitely known to be of polyembryonic habit, with their hosts and the number of individuals developing in each one, are given in the following list.

ENCYRTIDAE OF KNOWN POLYEMBRYONIC HABIT

Species	Host	Max. no. in one host	Authority
Ageniaspis atricollis Dalm	*Argyresthia pruniella* L.	22	Jancke (1932)
Ageniaspis fuscicollis Dalm	*Hyponomeuta* spp.	180	Marchal (1904)
Ageniaspis fuscicollis subsp. *praysincola* Silv.	*Prays oleelus* F.	19	Silvestri (1908)
Ageniaspis testaceipes Ratz	*Lithocolletis cramerella* F.	15	Marchal (1904)
Copidosoma boucheanum Ratz.	*Hyponomeuta*, etc.	39	Parker and Thompson (1928)
Copidosoma buyssoni Mayr	*Coleophora stefanii* Joan.	119	Silvestri (1914*a*)
Copidosoma gelechiae How	*Gnorismoschema gallaesolidaginis* Riley	234	Leiby (1922)
	Gnorismoschema salinaris Busck	395	Patterson (1915)
Copidosoma nanellae Silv	*Recurvaria nanella* Hbn.	11	Silvestri (1923)
Copidosoma thompsoni Mercet	*Nothris senticetella* Staud.	18	Parker and Thompson (1928)
Litomastix kriechbaumeri Mayr	*Depressaria alpigenella* Frey	120	Ferriere (1926*b*)
Litomastix truncatellus Dalm.	*Phytometra brassicae* Riley	3000	Leiby (1926, 1929)
	Phytometra gamma L.	2320	Silvestri (1907)
Litomastix floridanus Ashm.	*Phytometra brassicae* Riley	2028	Patterson (1917)

In addition, there are a number of other species in which the evidence, though not as yet conclusive, points strongly toward the same type of reproduction. Among these, the following may be mentioned:

Species	Host	Max. no. in one host	Authority
Berecyntus bakeri How.	Noctuid larvae	1705	
Copidosoma geniculatum Dal	*Rhyacionia buoliana* Zell.	24	
Copidosoma pyralidis Ashm.	*Anarsia lineatella* Zell.	104	
Copidosoma tortricis Waterst.	*Oxygrapha camariana* Zett.	53	Silvestri (1923)
Copidosoma sp.	*Olethreutes variegana* Hbn.	116	Sarra (1918)
Encyrtus mayri Masi.	*Oecophyllembius neglectus* Silv.	17	Silvestri (1908)
Paralitomastix variicornis Nees . .	*Anarsia lineatella* Zell.	28	Sarra (1915)

The genus *Encyrtus*, as now restricted, is limited in its host preferences to nondiaspine Coccidae, and the species listed above under that genus probably belongs instead in one of the genera included in the first list. Ishii (1932*a*) records the finding of what he believes to be an embryo chain of *Syrphophagus* sp. in the larva of a syrphid fly.

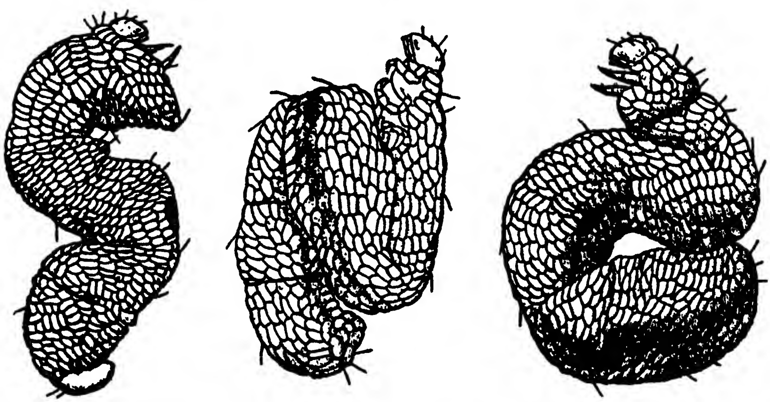


Fig. 71.—Larvae of *Phytometra gamma* L. parasitized by *Litomastix truncatellus* Dalm., showing the characteristic inflated and distorted condition following pupation of the vast number of parasites within the body. (*From Silvestri*, 1906.)

For detailed accounts of embryological development in species that undergo polyembryonic reproduction, the reader is referred to the publications by Marchal, Silvestri, Martin, Patterson, and Leiby. The parasite egg is deposited within the embryo in the host egg and during the remainder of incubation of the latter, and in the body of the developing caterpillar, it multiplies into a varying number of cells, forming an elongate, asymmetrical body, enveloped in a membrane of parasite origin, the whole mass being generally referred to as an "embryo chain"

(Fig. 72). This chain, which is free-floating in the body of the caterpillar, finally breaks up into its component parts, each of which becomes attached to a host organ and develops into an embryo and finally into a larva. This latter stage is attained only after the host larva has become mature. In hosts that produce a very large number of parasite individuals, several of these embryo chains may be found, each one of which has developed from a single egg.

The sexual, or normal, larva is hymenopteriform and presents no distinctive features. Among the larvae arising from an embryo chain, there are, however, a varying number that are characterized by the lack of the reproductive, the respiratory, and possibly the circulatory system. These, which have been designated as asexual larvae (Fig. 77*B*), were first observed by Silvestri in *Litomastix truncatellus* and have since been

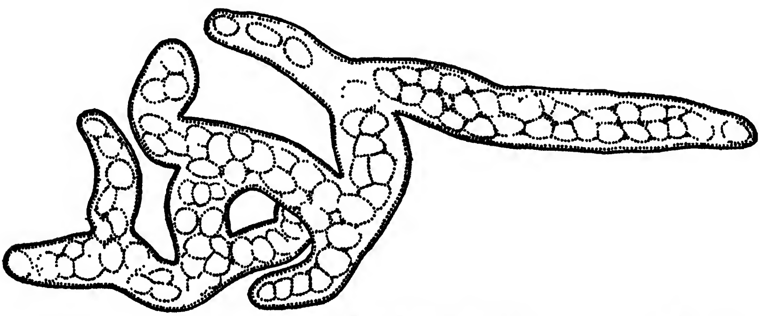


FIG. 72.—A branched embryo chain of *Ageniaspis fuscicollis* Dalm. at the stage when the full complement of morulae have been developed. (*Redrawn, after Marchal*, 1904.)

found among the broods of many other species. They develop in advance of the sexual larvae and are of greater size. They are unable to feed directly and begin to disintegrate shortly after emergence from the embryonic envelope. Silvestri has expressed the opinion that these larvae serve a definite purpose in lacerating or breaking up the host tissues for the feeding of the sexual larvae, but Parker and Thompson (1928) consider them to be mere monstrosities and of no special significance. Silvestri further presents the hypothesis that the asexual larva is an ancestral form, harking back to the time when the normal larva was free-living and somewhat vermiform.

The length of the life cycle of the polyembryonic Encyrtidae is dependent upon that of the host, inasmuch as larval feeding is not completed until the host larva is in its final instar. Most of the species listed have only one generation per year, though several have two or three. In the latter case, the cycle of the summer broods, from egg to adult, is approximately 30 days.

The manner in which the period of hibernation is passed is also dependent on the cycle of the host. *C. gelechiae*, parasitic in *Gnorismos-*

chema salinaris, passes the winter in the adult stage and oviposits in the spring as soon as host eggs become available whereas, when parasitic in *G. gallaesolidaginis*, this period is passed as an egg in the host embryo. Other species are found during the winter in their early stages of development within the partly grown host larvae, and still others are in the mature larval stage within the host carcass. In every species, there is a close synchronization with the cycle of the host.

The parasite brood that emerges from a single host may all be of the same sex, or they may be mixed. No males have thus far been found in *C. thompsoni* and in only one instance in *L. kriechbaumeri*. These two species may reproduce unisexually. In the majority of remaining species, the broods (the term "brood" is used to designate the total parasite content of a single host individual) are of one sex only, with, in some species, occasional broods containing a few individuals of the other sex also. According to Silvestri, the broods of *L. truncatellus* in *Phytometra gamma* are usually of one sex only, but Leiby (1926) found that the great majority of those from *P. brassicae* are mixed. *L. floridanus* and *Paralitomastix variicornis* normally produce a large majority of mixed broods.

The brood may arise from a single parasite egg, or it may be the result of several ovipositions. It has been noted in several species that several eggs are deposited at one insertion of the ovipositor. Silvestri states that about one hundred normal larvae are produced from each egg of *L. truncatellus*. The several thousand individuals in each brood must consequently be the result of a considerable number of ovipositions. Marchal and others have considered that the mixed broods are the result of oviposition by both mated and virgin females in the same host individual, the former producing female progeny and the latter male progeny only. This explanation has not been considered adequate by later authors, particularly Patterson.

Effect of Parasitism upon Host Reproduction.—A great many species of encyrtid parasites of Coccidae attack the adult females, but, if oviposition is in the nymphs, host death does not occur until after maturity is reached. The host consequently may be able to realize a portion of its reproductive potential, and the value of the parasite is correspondingly reduced. According to Ishii, *Microterys speciosus* exercises very little repressive effect upon the increase of *Ceroplastes rubens* Mask., for death of the parasitized female seldom occurs until the full quota of eggs has been deposited. In contrast to this, *M. clauseni*, in its spring generation upon adult *C. floridensis* Comst., very largely inhibits oviposition after the parasite eggs are laid, and the portion of the oviposition potential that is realized in the field is small.

It has been estimated by Imms (1918*a*) that 71.9 per cent of the females of *Eulecanium coryli* L. parasitized by *Blastothrix sericea* deposit

approximately their normal quota of eggs. Females of *Lecanium kunoensis* parasitized by *Encyrtus infidus* in Chosen were estimated to deposit about 50 per cent of the normal number, and it was noted that oviposition frequently takes place even after the parasites within the body have attained the pupal stage.

The effect of parasitism upon the diaspine scales is more quickly evident. Taylor (1935) states that the disintegration of the body of *Aspidiotus destructor* Sign. begins immediately after hatching of the eggs of *Comperiella unifasciata* Ishii and *Spaniopterus crucifer* Gahan; consequently, oviposition ceases within five days after attack by these parasites.

Life Cycle.—The great majority of species of the family produce several generations each year. This is particularly true of those whose hosts are in a proper stage for attack throughout the season. Under optimum temperature conditions, the cycle from egg to adult is complete in two to seven weeks. *Ooencyrtus malayensis* Ferr., parasitic in the eggs of Pentatomidae in Java, completes its cycle in 12 to 13 days.

In many cases, the duration of the life cycle is strictly dependent upon that of the host. This is particularly true of the polyembryonic forms that oviposit in the host egg and emerge from the mature larva or the prepupa. A given species may have a single annual generation upon one host and several upon another, depending upon the habits of the hosts. In each case, the cycles are closely synchronized.

Among those species that are parasitic in scale insects, several generations per year is the rule, though notable exceptions occur. *Microterys clauseni*, which passes through its spring generation in *Ceroplastes* in approximately one month, nevertheless has only two generations annually. These adults must persist in the field for several months until the young scales are sufficiently developed for attack in the autumn. Hibernation may be in any larval or even in the pupal stage within the host.

Many of the species that parasitize insect eggs have a life cycle entirely independent of that of the host. Thus, *Ooencyrtus kuvanae* has six and a partial seventh in the eggs of the gypsy moth, though the latter has an annual cycle, the greater portion of the year being passed in the egg stage. The parasite itself hibernates as an adult.

IMMATURE STAGES

The Encyrtidae reveal an exceptional diversity in form of the immature stages, and many of the modifications are strictly adaptive. These are made necessary not only by the wide range of hosts attacked, but by the varied conditions under which development takes place.

The Egg.—Two general types of egg are produced by the Encyrtidae, these being the stalked and the encyrtiform, the latter representing an adaptive modification of

the first. In both forms, the ovarian egg is two-bodied, and the contents of the anterior body, or bulb, are forced into the egg proper at the time of oviposition, leaving the stalk as a slender tube at the anterior end. In the stalked form, this stalk is functionless after deposition but may, in some instances, serve to attach the egg to the integument or to one of the internal organs of the host. Representative genera having this type of egg are *Aphidencyrtus*, *Cerapterocerus*, *Eusemion*, and *Anarhopus*. In *Tetracnemus pretiosus*, according to Clancy, the stalk is reduced to a broad, blunt petiole one-third to one-fourth the length of the egg body.

The encyrtiform egg is distinguished from the stalked form by a heavy surface rib, termed the aeroscopic plate by Silvestri (1919), which extends the length of the stalk and of the greater portion of the egg itself. Well-known genera having encyrtiform eggs are *Encyrtus*, *Microterys* (Fig. 73*A*, *B*), *Aphycus*, *Metaphycus*, *Blastothrix*, and *Ooencyrtus*. The plate of *O. johnsoni* is described by Maple as granulate in appearance and is composed of a mosaic of cells upon the outer surface of the stalk and egg

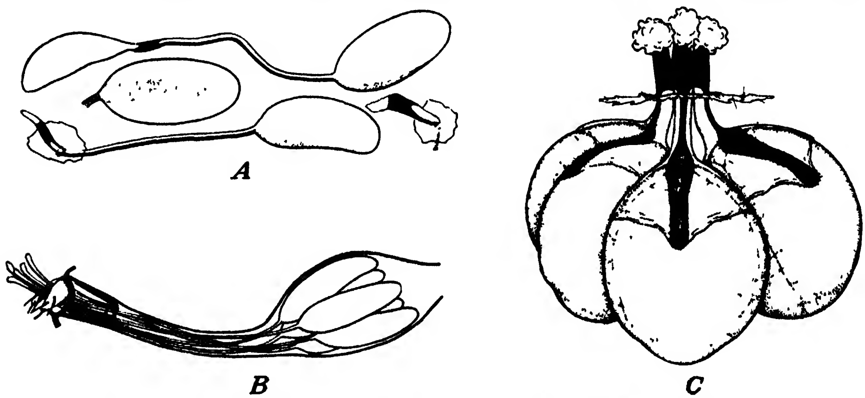


FIG. 73.—*A*, Ovarian and laid encyrtiform egg of *Microterys lunatus* Dalm., showing details of the aeroscopic rib (*from Silvestri*, 1919); *B*, a cluster of eggs of *M. clauseni* Comp. *in situ* in the intestine of *Ceroplastes floridensis* (original); *C*, a group of encyrtiform first, instar larvae of *Isodromus niger* Ashm., showing the posterior portion of the body of each closely enveloped by the eggshell. The stalks of the eggs protrude through the skin of the host and through them the respiratory requirements of the larvae are met (*drawing by D. W. Clancy*).

body except for a thickened area near the base of what remains of the bulb of the ovarian egg. In deposited eggs, the plate is much darker than the remainder of the chorion.

In two species of *Isodromus* parasitic in *Chrysopa* larvae, it has been found by Clancy that the egg of one, *I. niger* Ashm., is typically encyrtiform, whereas the other, *I. iceryae* How. (Fig. 74), lacks the aeroscopic plate and bears merely a melanized ring and a delicate membranous collar on the stalk.

First-instar Larvae.—Among the monembryonic species of the family, four forms of first-instar larvae may be distinguished, based upon morphological modifications having a functional nature. The hymenopteriform larva has a body of 12 or 13 visible segments, is widest in the thoracic or anterior abdominal region, and has no sculpturing or segmental processes. These larvae lie free in the body cavity of the host and lack the open tracheal system. A typical representative of this group is *Comperiella bifasciata* How. (Compere and Smith, 1927).

The second is the encyrtiform, so called because it hatches from the encyrtiform egg previously described. The number of body segments is reduced, there being

only 10 or 11 visible, and the last segment, which bears the single pair of spiracles, apparently represents several that have fused. The last four or five segments are usually closely enveloped by the eggshell, and this connection persists through the greater portion of the larval stage. The larva of *Isodromus iceryae*, which hatches from the modified encyrtiform egg already described, is hymenopteriform, for it lacks the posterior spiracles and consequently does not derive its air supply through the stalk. Both the egg and first-instar larva of this species appear to represent transitional stages between the hymenopteriform and the encyrtiform type. The genus *Microterys* contains many well-known species having encyrtiform larvae; yet it has been shown by De Bach that in *M. titiani* it is hymenopteriform, with a full complement of spiracles.

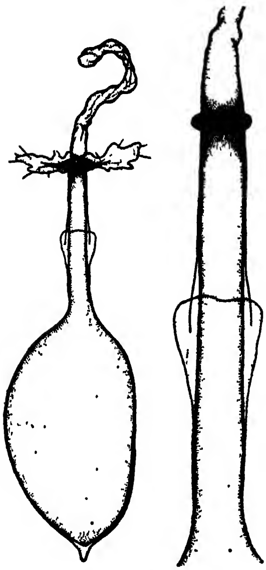


FIG. 74.—The egg of *Isodromus iceryae* How., an unusual form in which the modified stalk projects through the host skin, yet it lacks the aeroscopic rib. At right a portion of the stalk showing adaptive structures. (*Drawing by D. W. Clancy.*)

The caudate larva (Fig. 77*A*) is frequently found among the species attacking Coccidae and Aphididae and is characterized by the development of the last abdominal segment into a tail-like organ that may exceed the body proper in length and may bear setae on the distal portion. It is associated with the stalked type of egg. These larvae do not possess open spiracles. Many genera have larvae of this type, the best known being *Aphidencyrtus*, *Cerapterocerus*, *Cheiloneurus*, *Eusemion*, etc.

The vesiculate form is similar to the hymenopteriform, except that the proctodaeum is evaginated to form a caudal vesicle. This modification is rare among the Encyrtidae and is at present known only in the genera *Anarhopus* and *Clausenia* (Fig. 76*C*), both of which parasitize mealybugs. *Tetracnemus pretiosus* (Fig. 76*A*, *B*) may be of the same type, though it is uncertain whether or not the small expanded organ on the caudal segment corresponds to the vesicle in the above-named species. Both *A. sydneyensis* and *T. pretiosus* are distinguished from other known Encyrtidae by the presence of a ring of fleshy processes or protuberances on the first 12 body segments; and the former has also a single, curved medium process dorsally on the last segment, immediately above the vesicle.

Intermediate-instar and Mature Larvae.—The greatest diversification in form occurs in the first instar, and the succeeding forms tend to become more uniform as the final instar is reached. The hymenopteriform larva, which lies free in the body cavity of the host, progresses through the series of molts without appreciable change in its essential characters. In the caudate forms, the tail becomes considerably reduced in size in the second instar and practically disappears in the third. The vesiculate forms, on the other hand, show an enlargement of the vesicle in the second and third instars. In *Anarhopus* and *Tetracnemus*, the ring of fleshy protuberances on each body segment of the first-instar larva is lacking after the first molt.

The number and position of the spiracles of the larvae are an exceedingly variable character in this family. In the hymenopteriform larva, the spiracles are lacking in the first and second instars, but they appear on the second to the tenth body segments in the third or a later instar. Among the species having caudate larvae, *Cerapterocerus mirabilis* Westw. is stated to lack spiracles until the fourth instar, at

which time the nine pairs appear in the position already mentioned. In *Carabunia myersi* (Fig. 78), they are first found on what is stated to be the third and final instar, and only three in number, the anterior pair being on one of the thoracic segments

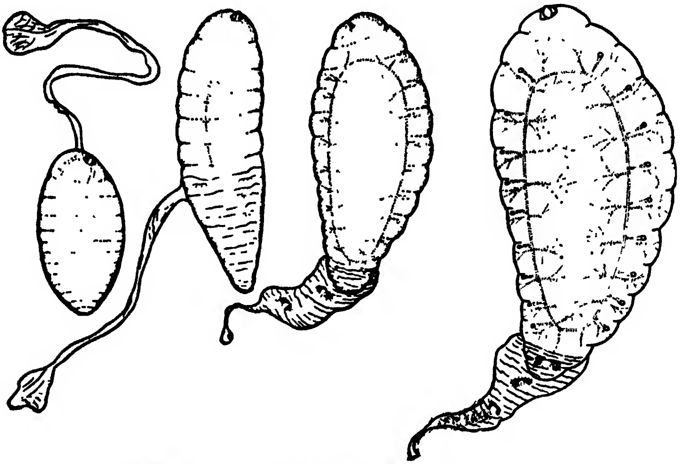


FIG. 75.—Immature stages of *Comperiella bifasciata* How. The egg (at left), with the embryo well developed, and the first-, third-, and fourth-instar larvae, showing the persistence of the exuviae about the posterior end of the body. (*From Compere and Smith*, 1927.)

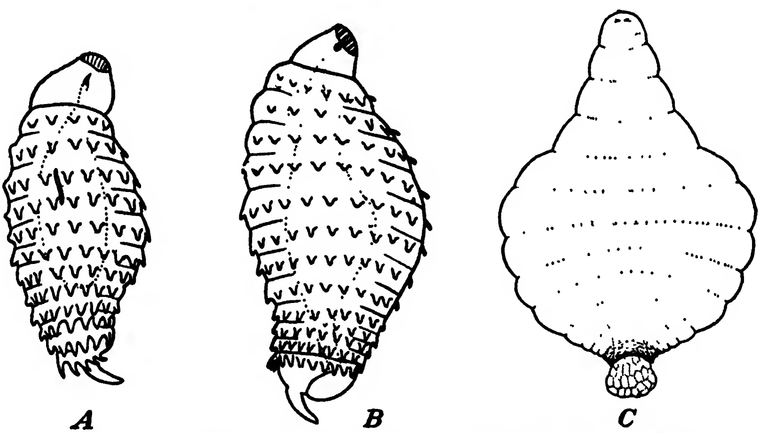


FIG. 76.—*A*, a newly hatched first-instar larva of *Tetracnemus pretiosus* Timb.; *B*, the same, just prior to the first molt, showing the anal vesicle; (*from Clancy*, 1934); *C*, a second-instar larva of *Clausenia purpurea* Ishii, showing the anal vesicle and the first larval exuviae encircling the last abdominal segment immediately in front of the vesicle (original).

and the remaining two pairs on the abdominal segments immediately preceding the caudal appendage.

Information regarding the spiracle arrangement of vesiculate larvae is available only for *Anarhopus sydneyensis*. In this species, they are lacking on the first instar and occur on the second to tenth body segments of the second and last instar. *Tetracnemus pretiosus* has no open spiracles until the final instar, when the full complement appears.

The first-instar encyrtiform larvae possess a single pair of spiracles on the last apparent abdominal segment. This arrangement persists in the following two instars, and the nine pairs of spiracles then appear on the fourth instar. In *Microterys speciosus* (Ishii, 1923), they are stated to appear on the third instar. Clancy mentions that the second instar of *Isodromus* is readily distinguished from the first by the presence of the spiracular spurs in the second to ninth body segments, and this character may be common to many second-instar larvae of the encyrtiform type. A marked departure from the normal for the family occurs in *Metaphycus lounsburyi* (Smith and Compere, 1920), in which the single caudal pair of spiracles of the first instar is followed by three additional pairs, situated on the second to fourth body segments, on the second instar, and by the usual nine pairs on the third instar.

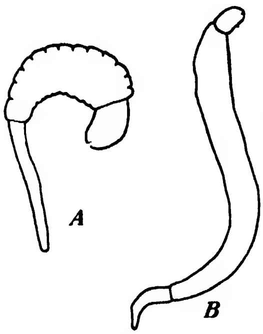


FIG. 77.—*A*, the caudate first-instar larva of *Baeoanusia oleae* Silv. (*from Compere*, 1931); *B*, the asexual larva of *Ageniaspis fuscicollis* Dalm. (*from Silvestri*, 1908).

A further modification in spiracular arrangement is found in certain species of *Encyrtus* having encyrtiform larvae, which acquire in their later stages an intimate connection with the host respiratory system. In *E. infelix* (Thorpe, 1936), the fourth instar has three pairs of spiracles, one of which is on the prothorax and the remaining two at the posterior end of the abdomen. The caudal spiracles are borne at the end of a pair of slender tube-like processes, merely enclosing the tracheal tubes, half to two-thirds the length of the body proper. The fifth-instar larva bears only two pairs of spiracles, one at each end of the body. This spiracular modification occurs also in *E. infidus*, though one instar apparently was overlooked, and the described third (Fig. 70*B*) is identical with the fourth of *E. infelix*. Ishii (1932*a*) describes the supposed first-instar larva of *E. barbatus* Timb. which has the three pairs of spiracles arranged in identically the same manner as is given above for the fourth instar. The large size of this larva indicates that it may be a later instar than that stated.

In considering the various adaptations, it is seen that the characters mentioned are common to a number of genera and that, in some instances, all species of a given genus do not reveal the same modifications.

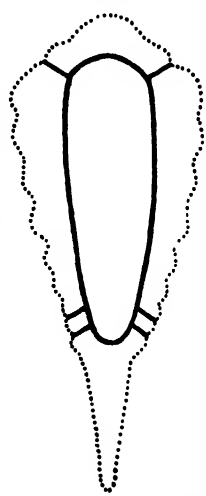


FIG. 78.—The tracheal system of the caudate third-instar larva of *Carabunia myersi* Waterst. (*After Myers*, 1930.)

CLEONYMIDAE

Very little information is available regarding the host preferences or relationships of members of this family. Observations have been made upon *Schizonotus sieboldi* Ratz. (Cushman, 1917; Dowden, 1939), *S. paillotti* F. & F. (Faure, 1926), and *Cheiropachys colon* L. (Russo, 1926, '38).

S. sieboldi is a gregarious external parasite of the pupae of *Plagiodera versicolora* Laich. and closely related chrysomalid beetles in the northeastern United States and Europe. The records given by

Dowden indicate that it is an important factor in holding these pests in check. The adult wasps pass the winter in protected places and attack the first brood of host pupae in the spring. In oviposition, the ovipositor is thrust beneath the pupa from the side, and one or several eggs are deposited on the thorax between the appendages, though occasionally upon the abdomen and some may even be placed upon the dorsum. Feeding by the adult female is upon the body fluids that exude from a puncture made in the dorsum after oviposition. This is one of the relatively few parasite species that develop externally upon exposed hosts, though the larvae occur between the body of the fixed host and the leaf so that conditions simulate the confined quarters of a cocoon or burrow.

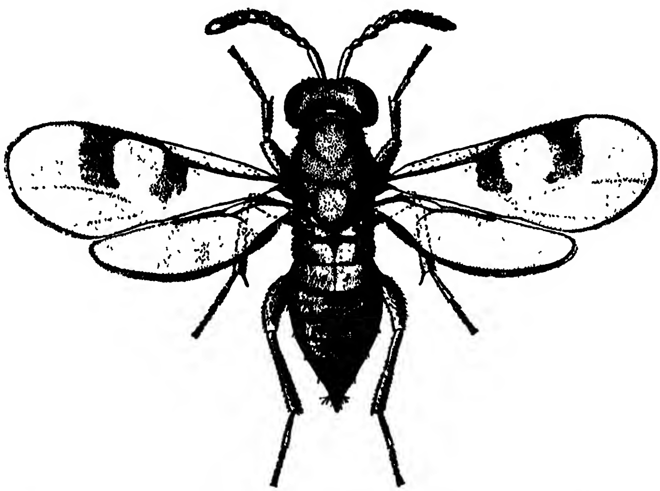


FIG. 79. The adult female of *Cheiropachys colon* L. (*From Russo*, 1938.)

S. paillotti of Europe differs in habit from *S. sieboldi*, it being a hyperparasite of various Lepidoptera through *Apanteles*. It is a solitary external parasite of the mature larva in the cocoon. The female feeds upon the host body fluids prior to oviposition and utilizes a feeding tube for this purpose.

C. colon L. is a solitary external parasite of the mature larvae of various Scolytidae in Europe. The host is paralyzed at the time of oviposition, and the relatively large egg is deposited upon the body. The sex ratio shows a preponderance of females to the extent of 5.5 to 1.

IMMATURE STAGES

The eggs have been described for only the three species previously mentioned. Those of *S. paillotti* and *S. sieboldi* are elongate-oval or somewhat cylindrical in out-

line, and that of *C. colon* (Fig. 80*A*) is narrowed at both ends, with the anterior end drawn out into stalk-like form and at times folded back upon the main body after deposition. In *S. paillotti* and *C. colon*, the chorion is clothed with minute spicules, though sparsely so in the last-named species, whereas *S. sieboldi* bears instead a fine reticulation on one side.

The first-instar larvae of the family are hymenopteriform, with small sensory setae and the integumentary setae may be uniformly distributed or in bands at the segmental margins. The respiratory system is equipped with spiracles on the mesothorax and first three abdominal segments.

The second- to fifth-instar larvae present no distinctive characters. The sensory setae and integumentary spines are minute. Nine pairs of spiracles appear on the fifth instar, these being situated on the second and third thoracic and the first seven abdominal segments.

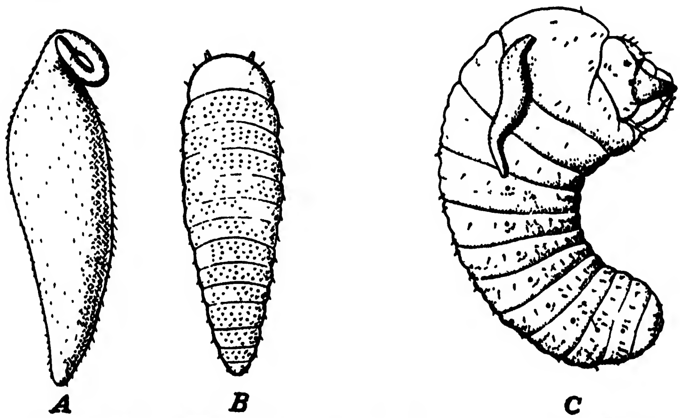


FIG. 80.—Early stages of *Cheiropachys colon* L. *A*, the egg; *B*, the first-instar larva; *C*, a scolytid larva bearing an egg of *Cheiropachys* upon the thorax. (*From Russo*, 1938.)

SIGNIPHORIDAE

The Signiphoridae is a small family, closely related to the Aphelinidae, comprising only a few genera and species. The various species are reared most commonly from dactylopiine, diaspine, and lecaniine Coccidae and Aleyrodidae, but several have been secured from Chermidae, and an occasional one has been obtained from the puparia of parasitic Diptera.

The host relationships have been definitely determined for only a few species. They had been assumed to be primary parasites, but those upon which close observations have been made have proved to be hyperparasitic in habit. It is probable that the great majority of representatives of the family develop in this way.

Thysanus elongatus Gir. is a gregarious, external hyperparasite of *Pseudococcus maritimus* Erh. through several Encyrtidae (Clausen, 1924). The advanced larval and pupal stages are attacked, though occasionally even a newly transformed adult, still within the remains of the host, may be parasitized and development completed upon it. Oviposition

takes place only on hosts that are contained in a thoroughly hardened secondary host shell. Either the female stands upon the "mummy" and inserts the ovipositor perpendicularly, or she may penetrate the side by a series of backward thrusts. The ovipositor may remain inserted for an hour or longer, and during this period 4 or 5 eggs are deposited upon the body of the host, to which they adhere closely. An examination of the ovaries of gravid females reveals only 3 to 6 fully developed eggs. This apparently represents the daily capacity, and all are normally placed on a single host. The maximum oviposition secured was 27, extending over a period of 13 days.

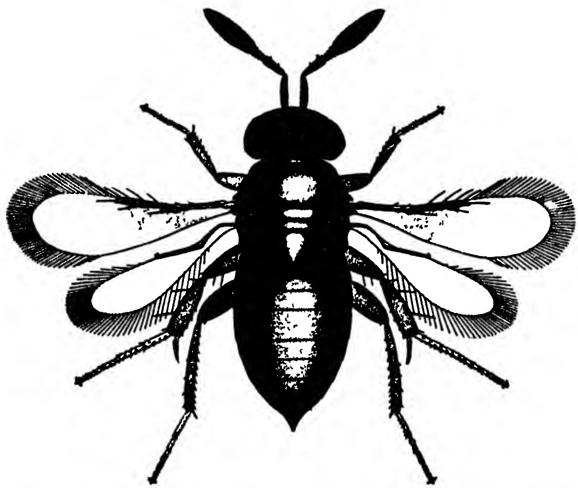


FIG. 81.—The adult female of *Thysanus elongatus* Gir. (*From Clausen*, 1924.)

The egg is 0.22 mm. in length, 0.07 mm. in maximum width, elongate-oval in form, and slightly curved, and bears a distinct peduncle at the anterior end. This egg is exceptionally large in relation to the size of the parent female, which measures only 0.7 to 0.9 mm. in length. Upon the completion of larval feeding, the meconium is cast, and a portion of it serves to attach the tip of the abdomen of the pupa to the wall of the cell. The cycle from egg to adult is completed in 25 to 30 days at summer temperatures. Hibernation takes place in the mature larval or pupal stage within the host remains.

Parthenogenetic reproduction results in male progeny only. The sex ratio of adults reared from field-collected material was 4.9 to 1, the females predominating.

EUPELMIDAE

The family Eupelmidae comprises a number of genera of common occurrence, the most frequently encountered being *Anastatus* and *Eupel-*

mus. *Anastatus* is essentially primary in its host relationships, and the various species attack the eggs of Lepidoptera, Orthoptera, and Hemiptera. With the exception of *A. amelophagus*, which is predaceous on *Ameles* eggs, all the known species that attack eggs are solitary and endophagous. Less frequently, they are found as solitary external parasites in dipterous puparia, particularly of the Tachinidae and Cecidomyiidae. However, as many as 15 individuals of *Anastatus viridiceps* Waterst. develop in a single tsetse-fly puparium in Africa.

The genus *Eupelmus* and others show a great diversity in habit; some are strictly primary external parasites, others are obligatory hyperparasites, and many appear indiscriminately in both roles. *E. cicadae* Gir., *E. excavatus* Dalm., *Lecanobius cockerelli* Ashm., and *Arachnophaga*

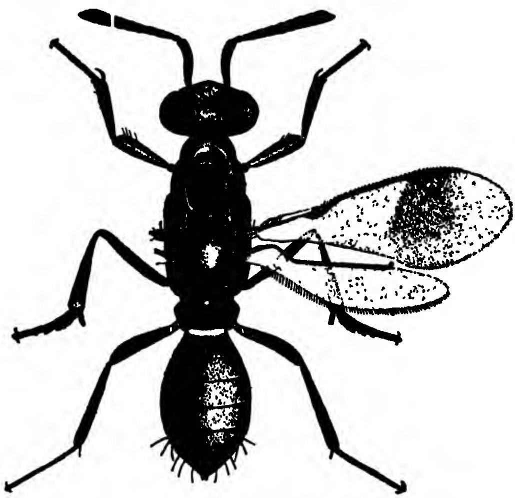


FIG. 82.—The adult female of *Anastatus albitarsis* Ashm. (*From Clausen*, 1927.)

picea How. are egg predators, the last in spider-egg sacs, though it has been reared also from *Chrysopa* cocoons as a hyperparasite. *E. popa* Gir. is predaceous upon the larvae and pupae of *Contarinia*. Various species are external parasites on the larvae of phytophagous Chalcidoidea; and *Eupelmella vesicularis* Ratz. (*Eupelminus saltator* Lind.), when developing as a primary parasite, is external upon the larva or pupa of the hessian fly within the puparium. *Calosota sinensis* Ferr. is a gregarious external parasite of the mature larvae of *Pareumenes*.

The wide range in host preferences of a single species is illustrated in the case of *Eupelmus urozonus* Dalm. This is an external parasite of the larva of the olive fly, *Dacus oleae* Rossi, in Italy, but it has been reared as a hyperparasite of the same host and from various other Hymenoptera, Diptera, Coleoptera, Lepidoptera, and Hemiptera (Silvestri *et al.*, 1908).

An exceptional number of the species of this family that are normal primary parasites have the habit of developing as hyperparasites also, at times on primaries not associated with the normal host. *Anastatus disparis* Ruschka, a parasite of gypsy-moth eggs, has been taken as an external parasite of the larvae of *Apanteles* in the cocoons, and *Anastatus pearsalli* Ashm., which normally attacks lepidopterous eggs, has also been reared from *Apanteles*. *E. spongipartus* Foerst., principally parasitic upon Cynipoidea, and *Eupelmella vesicularis*, a primary parasite of the hessian fly, have both been reared frequently from *Apanteles melanoscelus* Ratz. (Muesebeck and Dohanian, 1927). *Eupelmus tachardiae* How. is said to be a solitary internal parasite of the lac insect, *Laccifer lacca* Kerr, in India, but it develops also as an external parasite upon *Microbracon greeni* Ashm., which is parasitic upon a lepidopterous predator of the same scale insect (Glover *et al.*, 1936).

The capacity of a considerable number of species of Eupelmidae to develop consistently as internal parasites of their principal hosts, and as external parasites when in the hyperparasitic role, is noteworthy. This is an adaptation that is not common among insect parasites, and its significance is not clear. It brings to mind the recent discovery of the differential development of the sexes in *Coccophagus* and leads one to speculate on the possibility of a comparable phenomenon in this family. It could not, however, be exactly comparable in any case, for both sexes are produced upon the same host when development is internal.

The only species of the family thus far utilized in biological control work is *Anastatus disparis*, which was introduced into the United States from Japan and Europe in 1908–1909 for the control of the gypsy moth. Another species of the genus, *A. semiflavidus* Gahan, is being tested on a large scale in New Mexico, its native habitat, for the control of the range caterpillar, *Hemileuca oliviae* Ckll.

BIOLOGY AND HABITS

Habits of the Adult.—In 1874, Riley published a description of the habits of *Anastatus mirabilis* W. & R., the "back-rolling wonder." The female has the habit, common to many others in the family, of tumbling about after jumping and before gaining a foothold. The jumping habit is highly developed in this group and, rather than flight, is perhaps the chief mode of locomotion. In *A. amelophagus*, the females are apterous, and the males bear normal wings, whereas the females of *Eupelmella vesicularis* have the wings greatly abbreviated. Various degrees of wing reduction are found in other species as well.

A considerable number of species of the family that are parasitic in eggs have the habit of feeding upon the fluids that exude from the ovipositor puncture. Such feeding usually precedes oviposition; in

fact, stinging is frequently for feeding purposes only. D. L. Parker (1933) mentions the stinging of many host eggs by *A. disparis* without oviposition. It is probable that the habit increases very considerably the effectiveness of species that practice it. With most species, the female merely consumes the egg fluids that exude; but in the case of *A. disparis*, when feeding is upon the larva or pupa of *Ooencyrtus* within the gypsy-moth egg, a feeding tube is formed, which is true also of *Arachnophaga* when attacking *Chrysopa* cocoons. The female of *Anastatus axiagasti* Ferr. punctures the egg, feeds, and then wanders away; but she later returns, chews away the "cone" of dried fluids over the puncture, and reinserts the ovipositor for deposition of the egg (Lever, 1934).

The adults of *Eupelmus popa* appear to derive at least a portion of their food requirements from plant exudations (Woodruff, 1929). They were noted to feed upon the hairy tips of feterita heads on which they were ovipositing. These tips are bound together with a gummy fluid not found elsewhere upon the plant.

In *A. albitarsis* and others of the true egg parasites, it has been noted that when oviposition occurs in eggs in which some embryonic development has taken place the parasite egg is never placed within the embryo but is free-floating in the fluids that surround it.

The female of *A. albitarsis* spends 15 to 30 minutes in penetrating the heavy chorion of the egg of *Dictyoploca*, and initial penetration of the interior is exploratory in nature. An egg is never deposited in a host egg containing either a nearly mature host embryo or an advanced parasite larva.

The species that are external parasites may place the egg only in the vicinity of the host rather than directly upon it. In *Eupelmus allynii* French, about half the eggs are placed upon the inner wall of the *Harmolita* cell. *E. cicadae* places its egg in the egg chamber of *Cicada plebeja* Fall., but external to the eggs. The female of *E. popa* deposits them upon the hairs of the inner glumes of a spikelet of sorghum infested with *Contarinia sorghicola* Coq. *Lecanobius cockerelli* Ashm. inserts the ovipositor by a backward thrust beneath the margin of an egg-bearing female of *Saissetia oleae* Bern. and places her egg among those of the host.

Several species of the genus *Eupelmus* cover the egg with a fibrous network (Fig. 85*B*). This habit was first noted in *E. allynii* (Packard, 1916; Phillips and Poos, 1921), parasitic on the larvae of *H. tritici* Fitch, and about half of the eggs are covered in this way. The threads converge over the center of the egg, and it appears that the egg must first be laid upon the wall of the larval cell opposite the point of penetration by the ovipositor and the strands are then fastened to the cell wall around the margin of the egg and drawn up to the center. The material from which this covering is formed is probably derived from the colleterial glands of

the female parasite. This same type of egg covering has been noted also in *E. spongipartus*, *Eupelmella vesicularis*, and in *Eupelmus* sp. studied by Taylor (1937).

Among the various species that at times develop as hyperparasites, it has been noted that the egg stalk serves as an organ of attachment. The tip of the stalk of the *Anastatus pearsalli* egg is always embedded in the ovipositor puncture in the skin of the *Apanteles* larva (Muesebeck and Dohanian, 1927). The eggs of *Eupelmella vesicularis* deposited in *Diprion* cocoons are invariably found with their stalks fixed to the fibrous inner lining of the cocoon at the point of perforation. They are thus suspended above the mass of *Microplectron* larvae and are protected from injury during incubation.

The oviposition period is comparatively short and the reproductive capacity apparently low, at least in the few species of the family for which figures are available. The females of *Anastatus albitarsis* deposit an average of about 50 eggs during a period of 15 days, and *Eupelmella vesicularis* is reported to average only 20.

Larval Development.—The first-instar larva of *A. albitarsis* is able to move about readily in the semifluid contents of the host egg by repeated flexing of the body in the dorsoventral plane, and the bifurcate caudal process, in conjunction with the ventral rows of spines, aids materially in movement through such a medium. Although the need for such adaptations is limited when the larva is confined within an egg, yet they may be of considerable use to those species in which development takes place externally upon larval hosts. In the species of *Eupelmus* and other genera that are external parasites of larvae in plant cells or in cocoons, movement is between two plane surfaces, and the long, stout spines may consequently serve a locomotory function. In the succeeding instars, there is less need for change of position and these characters are lacking.

In *Eupelmus cicadae*, the egg is deposited in the egg chamber of *Cicada* but external to the eggs (Silvestri, 1918). The larva passes from one egg to another, sucking out the contents of each. The eggs in two or more chambers, situated close together in the twig, may be consumed by a single larva. The mature larva forms a channel or tunnel through the twig and, when this is completed, orients itself with the head toward the opening.

The larvae of *E. popa* are predaceous upon the larvae and pupae of the sorghum midge, *Contarinia sorghicola* (Woodruff, 1929). The newly hatched larvae of *Eupelmus* crawl from the hairs on the inner glume of the spikelet, where the eggs are laid, and search for midge larvae in the spikelet. The first-instar larva is able to feed only upon midge larvae, whereas the later instars attack the pupae, also. Some larvae

complete their development on a single host, but others require two or three. A portion of the larvae, after feeding upon one host, complete their growth upon plant sap, and these individuals lose the reddish color that is characteristic of larvae that continue the entomophagous mode of feeding. They may be found embedded in cavities, usually many times their own size, and surrounded by shredded plant tissue resulting from lacerations of the seed during the feeding period. This is the only known instance of plant feeding in the family, and the species is considered to be in an early transitional stage from an entomophagous to a phytophagous habit.

E. atropurpureus Dalm. is an external parasite upon the mature larva of *T. incertus* Ratz. when the latter occurs singly in its host, but when a number are present within the remains of the alfalfa-weevil larva, as is normally the case, it becomes a predator and consumes several or all of those which are present (Chamberlin, 1925). The habits of *Eupelmella vesicularis*, as described by Morris (1938), are similar. The egg is deposited in a *Diprion* cocoon containing larvae or pupae of *Microplectron fuscipennis*, the latter ranging in number up to 100 or more. From 10 to 20 of these are consumed during the larval feeding period, at the end of which time the *Eupelmella* larva enters its most destructive phase and kills every *Microplectron*, of whatever stage, including adults, contained in the cocoon. Thus, its repressive effect upon the latter is much greater than its size and numerical abundance would indicate.

The larval habits of *Eupelmus* sp., studied by Taylor (1937), present several features of interest. This species is normally a solitary external parasite of *Elasmus* and *Tetrastichus*, which develop upon the larvae of coconut leaf miners, *Promecotheca* spp., but it may develop as a primary parasite upon the latter, also. The newly hatched larva is very active and may move about through the leaf mine and feed upon several of the chalcidoid larvae if more than one is present. In case of attack upon a primary larva that has not completed feeding, the *Eupelmus* larva consumes it and then continues its feeding upon the leaf-beetle larva. Maturity can be attained after feeding upon only a single larva of *Elasmus*, but full-sized individuals arise only from larvae that have devoured several hosts.

The Life Cycle.—Incubation of the egg usually requires two to five days at summer temperatures, but this period may be greatly prolonged, and Caffrey (1921) states that a portion of the eggs of *A. semiflavidus* persist through the winter. The period from egg deposition to larval maturity covers only 10 to 20 days in most species, and the winter is passed as a mature larva or prepupa. *A. semiflavidus*, however, hibernates most commonly as a partly grown larva, and feeding is completed in the spring.

The majority of species studied have only a single generation each year, which corresponds to the cycle of the host. *A. albitarsis*, however, normally produces a partial second brood in the infertile *Dictyoploca* eggs that remain after the healthy eggs have hatched, and several alternate hosts are known that are in the egg stage during midsummer. *A. axiagasti*, parasitic in pentatomid eggs in the Solomon Islands, completes its cycle in 16 days and presumably has a large number of generations each year. In *A. semiflavidus* and *Eupelmus cicadae*, a portion of each brood persists in the larval stage until the second year. Irrespective of the length of the full cycle, the period devoted to actual feeding is always relatively short, ranging from one to two weeks.

Sex Ratio and Parthenogenesis.—Little information is available regarding variations in the reproductive habits of the Eupelmidae. Several species of *Anastatus* are known to show a slight preponderance of females, ranging up to 2 to 1 under normal field conditions, and parthenogenetic reproduction results in male progeny only. No males of *Eupelmella vesicularis* have been found in North America and females produce the same sex, generation after generation, whereas in Europe the males are abundant.

IMMATURE STAGES

There is little variation in form among the eggs of the representatives of the family. The main body of the egg is ellipsoidal and bears a stalk of varying length at the anterior end. In *A. albitarsis* (Fig. 83*A*), this stalk is only one-third the length of the egg body and is robust and turgid after deposition. There is no pedicel or flagellum at the posterior end, but only a minute tubercle. In other species of this genus and in other genera, the stalk is longer, at times equaling or slightly exceeding the egg body, and more slender and there is a tapering "flagellum" at the opposite end of the egg (Fig. 85*A*). After deposition of the egg, the stalk is usually convoluted or sharply bent. The eggs of this family are relatively large, ranging from 0.3 to 0.7 mm. for the length of the main body.

The first-instar larvae of the genus *Anastatus* are distinguished by a rather elongate form and the development of the last abdominal segment into a bifurcate process. The extreme modification in form within the genus is revealed by *A. albitarsis* (Fig. 83*B*), found in lepidopterous eggs (Clausen, 1927). The paired processes of the tail are curved and heavily sclerotized and lie at right angles to the plane of the body. The second and third thoracic and the first seven abdominal segments each bear a transverse row of long spines ventrally at the anterior margin. Those of the first row equal about three body segments in length, and they diminish in size on the successive segments. Other species of the genus show the above characters in a lesser degree (Fig. 84*A*), though in some the ventral spines are not arranged in a distinct row and do not appreciably exceed the dorsal spines in length.

The larvae of *Eupelmus* and other genera in which the first instar is known lack the bifurcation of the caudal segment and have a relatively small number of spines. That of *E. allynii* (Fig. 85*C*) has two pairs of long spines dorsally on each body segment except the last and one pair of smaller spines ventrally on each thoracic segment. The integument is densely clothed with minute setae. In *Arachnophaga*, one pair of

spines is dorsal and the second lateral, just beneath the line of the spiracles. The integument of the dorsum and side bears numerous peg-like projections. The larva

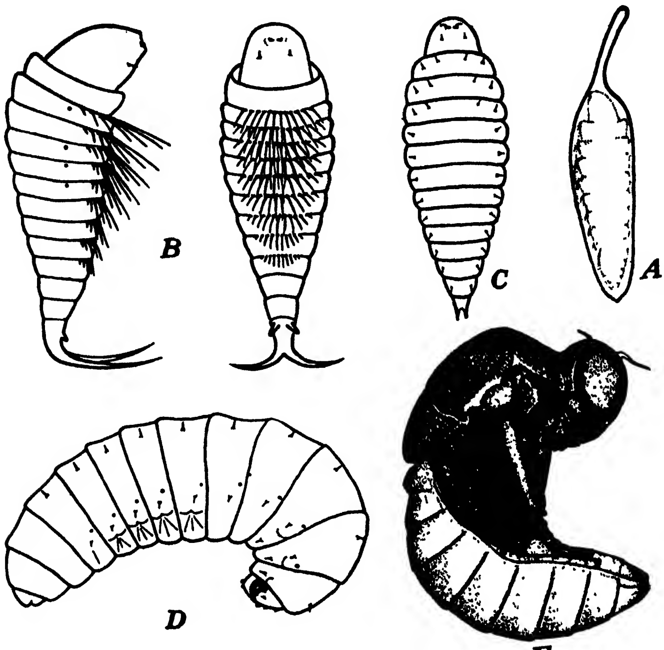


FIG. 83.—The immature stages of *Anastatus albitarsis* Ashm. *A*, the egg, containing a fully developed embryo; *B*, the first-instar larva, lateral and dorsal views; *C*, the second-instar larva; *D*, the mature larva; *E*, the pupa. (*From Clausen*, 1927.)

of *E. cicadae* is slender, with a large and heavily sclerotized head, and the segmental spines are very much reduced in size. That of *Eupelmella vesicularis* bears two pairs of long heavy spines on each body segment, with an additional shorter pair on each of the thoracic segments.

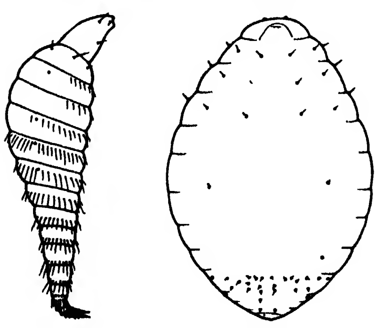


FIG. 84.—*A*, first-instar larva of *Anastatus* sp. (original); *B*, mature larva of *Anastatus* sp. (*from Parker*, 1924).

The tracheal system of this instar normally bears four pairs of spiracles, which are situated on the second thoracic and the first three abdominal segments. In *Eupelmus allynii*, however, an additional pair is found on the metathorax.

The studies made upon *Anastatus*, *Eupelmus*, and *Eupelmella* indicate that there are normally five larval instars, with the intermediate and final instars quite similar in form.

In *Anastatus*, there appear to be two forms of mature larvae, one being that of *A. albitarsis* (Fig. 83*D*) and *A. semiflavidus*, in which the body is robust, almost cylindrical, curved to conform to the egg in which it develops, and bearing only a few minute setae, and the other, represented by *A.*

disparis and *Anastatus* sp. (Fig. 84*B*), which is almost spherical in form. The latter bears short spines on the thoracic segments and a larger number on the sixth to ninth abdominal segments.

In *Eupelmus*, *Eupelmella*, and *Lecanobius*, the mature larva is rather elongate as compared with that of *Anastatus*. *Eupelmus allynii* (Fig. 85*D*) bears about seven pairs of long spines on the first thoracic segment, five pairs on the second and third, two pairs on the first five abdominal segments, and three pairs on the last five abdominal segments. Those on the abdomen are considerably shorter than the thoracic spines. Among the different species, the principal variation is in the size of these spines. The mandibles are simple. The number and position of the spiracles are constant in all the known genera, there being nine pairs, situated on the second and third thoracic and the first seven abdominal segments.

There is little variation in the form of the pupae within the family. Some have the body greatly curved, to conform to the outline of the egg in which they have

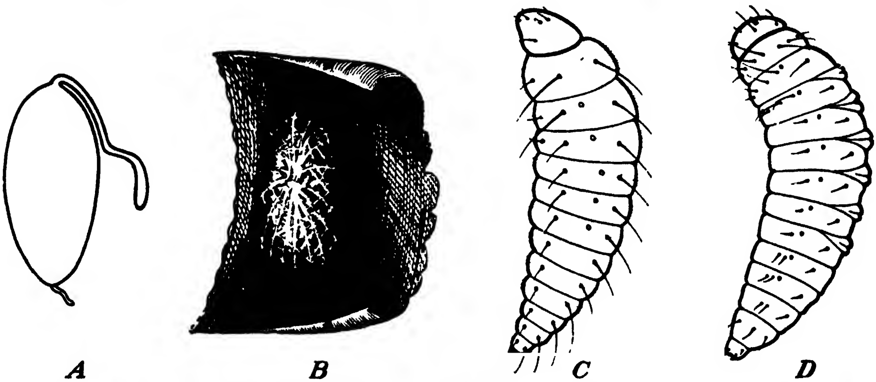


FIG. 85.—The immature stages of *Eupelmus allynii* French. *A*, the egg; *B*, an egg on the inner wall of the host puparium, showing the fibrous network with which it is often covered; *C* and *D*, first-instar and mature larvae, lateral views. (*A*, *C* and *D*, *from Phillips and Poos*, 1921; *B*, *from Packard*, 1916.)

developed, whereas others not so closely confined are more slender and the parts of the body are in the same plane. *A. albitarsis* is the only species known to possess the three fleshy processes on the head superimposed over the developing ocelli (Fig. 83*E*).

CALLIMOMIDAE

The family Callimomidae includes many phytophagous as well as entomophagous species, though the latter predominate. The majority of plant feeders are included in the genus *Megastigmus*, and several in *Callimome*, and development takes place in most cases within the seeds of various plants. The parasitic forms attack chiefly the immature stages of other insects in galls or seeds, or which bore into the stems of plants. According to Huber (1927), the genus *Callimome* in North America is known to include 40 species that attack the immature stages of Cynipoidea in galls and 25 species that are parasitic upon Diptera, largely the Cecidomyiidae. Several species of *Liodontomerus* are parasitic upon the larvae of seed-infesting Chalcidoidea. *Podagrion* differs markedly in

its host preferences and attacks the eggs of Mantidae. The great majority of species of the family are primary external parasites, though a number of species, particularly in the Monodontomerinae, show a wide range in adaptability and may develop in a hyperparasitic role also.

In biological control work, the only species that has been utilized is *Monodontomerus aereus* Wlk., which was imported into the United States from Europe from 1906 to 1910 in the attempt to control the brown-tail and the gypsy moths. Establishment was secured, but in the following years it became of more importance as a hyperparasite, through *Compsilura concinnata* Meig. and *Sturmia nidicola* Tns., than as a primary.

BIOLOGY AND HABITS

D. aureoviridis Cwf. which has been studied by Phillips and Poos (1921) as a parasite of the wheat jointworm, *Harmolita tritici* Fitch, and others of that genus in the eastern United States, may be considered as representative of the group attacking gall-making insects. It is a solitary external parasite of the mature *Harmolita* larva in the plant cell and at times develops as a secondary upon other primary parasites of the same host. The ovipositor is thrust through the wall of the wheat stem into the cell and the egg deposited upon the body of the host larva or in immediate proximity to it.

Several eggs may be deposited on a single host, but the oldest larva always destroys the remainder. The first-instar larva moves freely over the host and makes a number of feeding punctures. The body contents of the host are completely consumed, leaving only the empty skin, after which the meconium is cast and pupation takes place in the cell.

The cycle from egg to adult is complete in an average of 26 days, of which the egg, larval, prepupal, and pupal stages require 3, 11, 2, and 10 days, respectively. The minimum period noted for incubation was 1 day. There are normally two generations each year, though in some seasons a partial third develops in the field. The winter is passed in the mature larval stage in the host cell. A portion of the mature larvae of the first generation persist in that stage until the following spring.

Muesebeck (1931) has given an excellent account of the complex host relationships of *Monodontomerus aereus* Wlk. This species is a gregarious internal parasite in the pupae of the brown-tail moth, *Nygmia phaeorrhoea* Don., and of the gypsy moth, *Porthetria dispar* L. In addition, it occurs frequently as a hyperparasite, attacking a series of primary parasites of the above hosts. When developing in fully formed tachinid puparia, it is external, and this is true also when attack is upon hymenopterous larvae in cocoons, such as those of *Apanteles*, *Meteorus*, and *Hyposoter*. The latter hosts are usually killed by stinging at the time of oviposition. In very fresh tachinid puparia, where the larval hypo-

derm still adheres to the puparium, the eggs are deposited in the body cavity, but few of these individuals are able to reach the adult stage. Larval maturity is frequently attained, but conditions within the puparium are apparently unsuited for development beyond this point. The female parasite feeds extensively upon the body fluids of the different host stages mentioned above. To accomplish this, she forms a feeding tube from the host body to the outer surface of the pupa, puparium, or cocoon in which it is contained. A maximum of 24 individuals has been reared from a single *Compsilura* puparium.

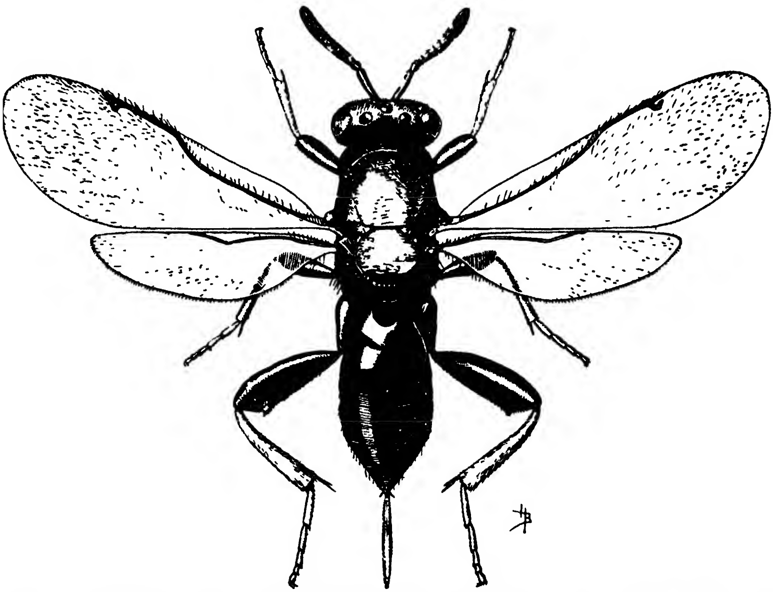


Fig. 86.—The adult female of *Monodontomerus aereus* Wlk. (*From Muesebeck*, 1931.)

The account of the biology and habits of *Epimegastigmus brevivalvus* Gir. recently presented by Noble (1938*b*) reveals several distinct departures from the normal for the family. It is a solitary internal parasite of the larvae of the citrus gall wasp, *Eurytoma fellis* Gir., in Australia. The female deposits her minute stalked egg within that of the host at virtually any stage of embryonic development. Its total length is very nearly that of the host egg, and consequently the stalk is usually found to be crumpled or bent back upon the egg body after deposition. The incubation period of *Eurytoma* is variable, ranging from 13 days to one month or more; but the parasite egg has a correspondingly long period of 34 to 39 days, and hatching consequently does not take place until after that of the host.

The host has an annual cycle, and larval development covers a period of approximately 10 months, of which about 8 months is required for the

first stage. For the first eight months of its life, the *Epimegastigmus* larva persists in the first stage also, and it is free-floating in the body fluids of the host. When activity is resumed in the spring of the following year, the host attains larval maturity while the parasite is still in its first stage; but the latter then accelerates its development and consumes the entire body contents before the host is able to pupate. At the completion of feeding, the larva emerges from the host skin and pupates in the cell of the gall.

The two features in the biology of *Epimegastigmus* that are distinctive are oviposition in the host egg and the synchronization of embryonic and larval development with that of the host. No other instance of this oviposition habit is recorded in the family; in fact, it is rare in the Chalcidoidea, being known only among the polyembryonic Encyrtidae and in a few species of *Tetrastichus*. The synchronization in development of parasite and host conforms to that which occurs not only in the groups mentioned above but in the Ichneumonidae, Braconidae, and Platygasteridae of similar habit. The prolongation of the first larval stage is common to all species having the same oviposition habit, but the protracted period of incubation in *Epimegastigmus* is a particular adaptation to ensure that the egg does not hatch until the host has attained the active first larval stage. The large size of the parasite egg in relation to that of the host in which it is placed is comparable to that of *Diplazon* in syrphid eggs and in sharp contrast to that of other parasites having the same habit.

In the genus *Podagrion*, which is apparently restricted in its host preferences to the eggs of Mantidae, the females have acquired the habit of attaching themselves to the female mantids in order to ensure access to the eggs as soon as they are laid. Bordage (1913) states that the female of *P. insidiosus* Coq. clings to the lower wings of the mantid until the time of formation of the ootheca, whereupon she descends into the frothy mass and oviposits. Several authors assert that oviposition can take place only at this time. C. B. Williams (1914) observed frequent oviposition by *P. pachymerum* Wlk. in egg cases of some age, and the parasite is therefore not entirely dependent upon the female mantid in locating them. There apparently is some doubt as to whether the species of *Podagrion* are egg predators or parasites. H. L. Parker (1924) states that *P. pachymerum* is an external parasite of the egg, whereas several other authors have described the position of the mature larva and pupa within the egg, indicating that it is a solitary internal parasite. Girault (1907) reared 240 adults of *P. mantis* Ashm. from 10 egg masses of *Stagmomantis carolina* L., a parasitization of 30.4 per cent as measured by the total emergence of parasites and young mantids.

The life cycles of the Callimomidae are usually relatively short, being completed in many instances in one month or less, but this does not necessarily result in the expected number of generations each year. *M. aereus*, with a cycle averaging only 22 days in length, usually produces only a single annual generation. A few species produce three or four generations each year.

The hibernation habit is variable, though the majority are probably in the mature larval stage during this period. *Monodontomerus aereus* is represented during the winter by adult females only. These are extremely hardy and have been known to live for at least 11 months. They enter the brown-tail-moth webs, to which they are attracted particularly by the empty pupal shells of the moth, as early as August and remain there, except for intermittent emergence during the autumn, until April or May of the following year. This is in contrast to the habit of *Epimegastigmus*, already discussed, of passing an equally long period in the first larval stage.

In all the species for which the sex ratio is known there is a preponderance of females, the extreme being 7 to 1 found by Urbahns in *Liodontomerus perplexus* Gahan. Parthenogenetic reproduction in *M. aereus* and in the majority of species of the family results in male progeny only, though according to Phillips and Poos (1927) the unmated females of *Eridontomerus isosomatis* Riley produce progeny of both sexes. The same authors, in their discussion of *Ditropinotus aureoviridis*, state that males do not occur in the first generation and that they are greatly outnumbered in those following. This implies a peculiar cycle wherein the overwintering larvae, which are the progeny of presumably mated females, develop into a brood of females only and these, though unmated, give rise to both sexes, with female progeny predominating.

The reproductive capacity of the parasitic species that attack gall-forming insects is low, as is to be expected from the protected situations in which they develop. *Epimegastigmus brevivalvus* deposits an average of about 140 eggs. The maximum recorded is 352 eggs from a female of *M. aereus* during a period of two months, and the average for this species is probably several hundred.

IMMATURE STAGES

The normal egg form in the Callimomidae is elongate-oval to kidney-shaped, with the anterior end broadest and terminating in a short, rounded protuberance. The posterior end is somewhat attenuated, and in occasional instances it terminates in a sharp point. The egg of *Epimegastigmus brevivalvus* described by Noble is markedly different, for it possesses a slender stalk about twice the length of the egg body. The illustrations of eggs of this species in different stages of embryonic development show the head of the larva at the end of the egg opposite the stalk, and the latter must

consequently be posterior, as opposed to its anterior position in the normal stalked egg of the superfamily. In this species and in *Callimome cyanimum*, the chorion is unsculptured and glistening, whereas in *Ditropinotus aureoviridis* (Fig. 87*A*), *Monodontomerus aereus*, *Eridontomerus isosomatis*, and *Callimome abbreviatus* it is densely clothed with minute papillae except, in some species, for a small area at the posterior end. These papillae often give the egg a grayish color.

The stalked type of egg described above for *Epimegastigmus* is of general occurrence among the phytophagous members of the family, though the stalk is normally at the anterior end.

The first-instar larvae are hymenopteriform, with 13 distinct body segments, and bear rather large, cylindrical antennae and sensory setae on the head, heavy and long sensory setae on the body segments, particularly the thorax, which may equal the length of several segments, and spiracles on the second thoracic and first three abdominal segments. Each body segment also bears a band of short integumentary setae.

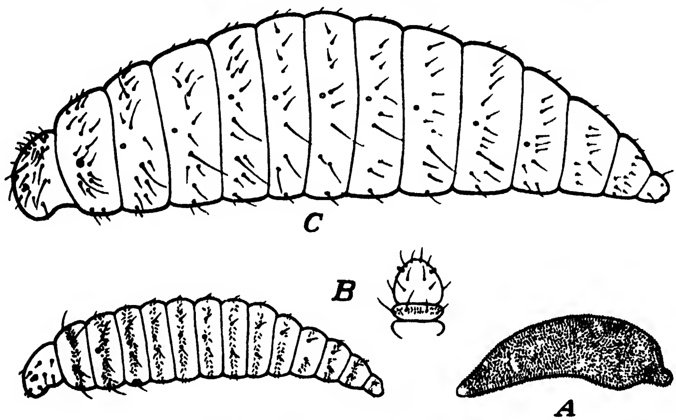


FIG. 87.—The immature stages of *Ditropinotus aureoviridis* Cwf. *A*, the egg; *B*, the first-instar larva, lateral view, with the head, dorsal view; *C*, the fourth-instar larva, lateral view. (*From Phillips and Poos*, 1921.)

Several species show departures in one or more characters from the above. The larva of *Epimegastigmus brevivalvus* is very stout, is devoid of sensory and integumentary setae, and has no spiracles or internal tracheal system. In *D. aureoviridis*, there are said to be five pairs of spiracles, the additional pair being on the metathorax, and there are indications of this pair in *Eridontomerus isosomatis*, also.

Five larval instars have been observed and described in *D. aureoviridis*, *E. isosomatis*, *M. aereus*, and *Epimegastigmus brevivalvus*. In the first two species, the second-instar larvae can be readily distinguished from the first by the reduction in size of the sensory setae and the absence of the bands of integumentary setae. The sensory setae then become progressively larger and the integumentary setae more abundant in the following instars. The full complement of spiracles appears on the second-instar larva, situated on the last two thoracic and the first seven abdominal segments. In *E. brevivalvus*, the internal tracheal system is first evident in the third instar, but open spiracles do not occur until the fifth.

The mature larva of the majority of species bears heavy and long sensory setae and one or more rows of long integumentary setae in a band encircling each segment, giving it a distinctly hairy appearance. In *D. aureoviridis* (Fig. 87*B*) and *Eridontomerus isosomatis*, the head is also densely clothed with setae and spines of varying

length. The larva of *Epimegastigmus brevivalvus* bears a closer resemblance to those of the phytophagous members of the family, the integument being smooth and shining except for a transverse row of very minute setae on each segment. That of *P. pachymerum* is distinguished by a heavy band of minute setae, set upon tubercles, on each segment.

In a considerable number of species, the mandibles of the fifth instar are simple, as are those of the earlier instars, but in *E. brevivalvus* they are tridentate, and in *Megastigmus dorsalis* F. and *Epibootania nonvitta* Gir. they are 4-dentate.

EURYTOMIDAE

The family Eurytomidae comprises many phytophagous as well as entomophagous forms. The dominant genus *Eurytoma* includes many species that develop in the seeds of plants, whereas *Harmolita* forms galls

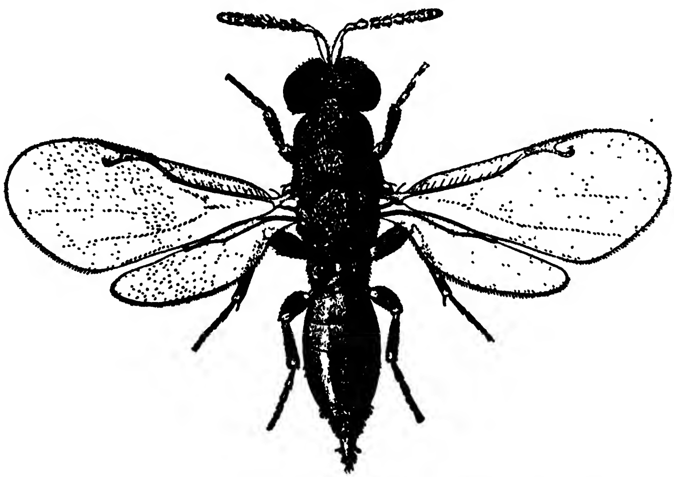


FIG. 88.—The adult female of *Eurytoma masii* Russo. (*From Russo*, 1938.)

in the stems of grasses and other plants. Several other less common genera are of similar habit. Well-known examples of phytophagous Eurytomidae are the wheat jointworm, *Harmolita tritici* Fitch, the wheat straw worm, *H. grandis* Riley, and the clover seed chalcid, *Bruchophagus gibbus* Boh. Gahan (1922) has given an account of the plant-feeding habit in this and related families and has enumerated the species of Chalcidoidea known to develop in this way. Several species are parasitic in their early stages and plant feeders later.

The information on the parasitic habits of the family is limited mostly to *Eurytoma*, which has diverse host preferences, some species being external parasites of the larvae of Hymenoptera (mainly Cynipoidea in galls), whereas others attack coleopterous, lepidopterous, and dipterous larvae in galls, tunnels, etc. Some species are strictly hyperparasitic in habit. Several species of *Eurytoma* depart from the cus-

tomary host relationships of the genus in being endoparasitic in the larvae of gall-making trypetid flies. *E. oophaga* is predaceous upon the eggs of *Oecanthus*, and species of the genera *Archirileya* and *Macrorileya* have the same host preferences. *Rileya* is recorded as attacking the larvae of Cecidomyiidae. *Conoaxima* is parasitic in or on the adult queens of ants of the genus *Azteca* inhabiting the fistulose stems of *Cecropia* (Brues, 1922), and *Axima* has been bred from the nests of the small carpenter bees.

BIOLOGY AND HABITS

E. parva Gir. (Phillips, 1927) is representative of the forms that attack gall- and stem-infesting hosts. Though it is in large part phytophagous, yet the habits and larval forms are typical of those which are strictly parasitic. It is a solitary external parasite of the first- or second-instar larva of *H. tritici* Fitch in the stems of wheat. Its parasitic phase covers only a short period, in the course of which the *Harmolita* larva is completely consumed, and development is then completed upon plant sap. Development to maturity may occur even upon sap alone. The species is essentially parasitic, however, inasmuch as the stimuli for oviposition are provided by the *Harmolita* larva rather than by the plant. According to Phillips "The larva of *Eurytoma parva* is at present in a highly plastic or adaptive condition, a fact which indicates to the writer that it is in the process of changing over from parasitism upon animals to phytophagy, while as yet entirely dependent upon *Harmolita tritici* for the stimulus leading to oviposition."

There is a single generation each year, and the winter is passed in the mature larval stage in the cell in the wheat stem. The adults emerge from the middle of May onward. The period of gestation is relatively long, for very few or no eggs are present in the ovaries at emergence. The females are long-lived and persist in the field for one month or more. When ready to oviposit, the female inserts the ovipositor through the wall of the wheat stem into the cavity occupied by the young *Harmolita* larva. The egg is placed only in the vicinity of the host larva and at times is outside the jointworm cell. Hatching occurs in four or five days, and the host larva is consumed by the first-instar larva, after which feeding begins upon plant sap in the host cell. There is considerable laceration of plant tissue in the course of this feeding, probably more than would have been done by the *Harmolita* larva, and a large amount of frass accumulates in the cell.

E. curta Wlk. develops internally in the larvae of the gall-making trypetid, *Euribia jaceana* Her., in England (Varley, 1937). The maggots are attacked when very young, and development of host and parasite progress concurrently until pupation of the former in the late summer.

Premature pupation at this time is due to the stimulus of parasitism, for healthy individuals do not pupate until spring. An identical reaction was observed by Hughes (1934) in the case of *Eurytoma gigantea* Walsh and *E. obtusiventris* Gahan, both of which are internal parasites of trypetid gall makers in goldenrod. This effect may prove to be of common occurrence; it has been noted also in Diptera parasitized by *Alysia* and *Brachymeria*.

Varley calls attention to the frequent occurrence, among the mature larvae of *E. curta*, of the habit of feeding upon plant tissue after the insect host has been consumed. The laceration of the wall of the cell is a constant feature in the case of this and several other species which parasitize gall-inhabiting larvae, though the phytophagous habit has not attained so high a degree of development as is found in *E. parva*.

The well-known *E. appendigaster* Dalm. of Europe is a secondary or tertiary parasite, through various Braconidae and Ichneumonidae, of a number of Lepidoptera and has also been reared from tachinid puparia (Faure, 1926; Rosenberg, 1934). The host is paralyzed by the sting, and a feeding tube is constructed through the cocoon wall, by means of which the body fluids are imbibed by the parasite adult.

An exceptional instance of adaptation to host habits is shown in *E. monemae* Ruschka of China (Piel, 1933*a*; Piel and Covillard, 1933), which is a gregarious external parasite of the mature larva of the oriental moth, *Monema flavescens* Wlk., in its cocoon. The female is unable to penetrate the thick, hard cocoon wall with the ovipositor and consequently must devise some other way to gain access to the host larva. This problem has been solved in a novel way, and through the intervention of another parasite. *Chrysis shanghaiensis* Smith, likewise parasitic upon this same larva, is directly concerned in the sequence of events leading to oviposition by *Eurytoma*. In the early broods, the *Eurytoma* female pays no attention to the *Monema* cocoons themselves but is attracted instead to the *Chrysis* female, which she follows persistently until her egg is laid. While the *Chrysis* is busily engaged in cutting away an opening in the cocoon and in laying the egg, which may require 15 to 60 minutes, the *Eurytoma* waits patiently near by. After the oviposition puncture has finally been closed, she approaches it, thrusts the ovipositor through the rather spongy plug, and deposits her own eggs, a process that may require a period of several hours. A maximum of 83 individuals have been found to develop on a single host larva, and all the adults emerge through the *Chrysis* oviposition puncture. The third generation of *Eurytoma* has no counterpart in *Monema* or *Chrysis*, which have only two generations; this brood consequently reproduces on the same host brood as the preceding generation, and the females are able to locate the parasitized cocoons and the plugged oviposition holes without aid.

Though *E. monemae* is essentially a primary parasite of *Monema* larvae, yet it is able to develop also as a secondary parasite, through *Chrysis*. As a primary parasite of *Monema*, the destruction of the egg or young larva of *Chrysis* is merely incidental. The above complex relationship, in which one parasite is forced to utilize the services of another to gain access to the host, is without parallel in this or other families. Aside from the attraction of *Eurytoma* to *Chrysis* adults, which is interesting but apparently not essential, the oviposition of the former and the emergence of its adults at maturity are both strictly dependent on the presence of the *Chrysis* oviposition hole.

E. oophaga Silv. develops as a predator upon the eggs of *Oecanthus pellucens* Scop. in Italy (Silvestri, 1920). The egg is laid near the anterior end of one of the host eggs in the egg chamber, and the first four larval stages derive their food supply from a single egg.

Archirileya inopinata Silv. has been studied by Silvestri as a predator upon the eggs of *Oecanthus* and other Orthoptera and Homoptera that place their eggs in incisions in twigs. Oviposition and early larval development are identical with those of *E. oophaga*. The fourth- and fifth-instar larvae, however, are very active; they may consume all the eggs contained in the *Oecanthus* chamber and may burrow 1 cm. or more through the pith of the plant stem to attack another egg cluster. The first generation develops upon eggs of *Cicada* and *Tettigia*, and the second is upon *Oecanthus*.

Macrorileya oecanthi Ashm. of North America, which develops upon the eggs of *O. niveus* DeG., differs somewhat in habit from *A. inopinata* (L. M. Smith, 1930). The host eggs are deposited in individual incisions in plant stems, and the parasite places its egg alongside the base of the host egg, with the long stalk extending the full length of the latter. After consuming the contents of the one egg, the parasite larva then burrows through the pith until another is found, and this procedure continues until 10 to 15 are located and consumed. The burrow constructed by the larva is smooth and free from frass, and its length is dependent upon the spacing of the *Oecanthus* eggs. In one instance, it was found to extend in a winding course for a distance of 37.5 cm.

Life Cycle.—The period from deposition of the egg to attainment of the mature larval form is relatively short in all species except those which develop internally in trypetid larvae, though the inactive portion of the last larval stage may be greatly prolonged. *Archirileya* reaches the mature larval stage 24 days after oviposition, of which 3 days is required for incubation of the eggs. *E. monemae*, in its summer broods, develops from egg to adult in 15 to 16 days. All species of the family that have been studied pass the winter in the mature larval stage, and they may persist in that stage until the middle of the following summer. The

normal time of emergence of the first brood of adults of *E. monemae* is during July, and this is the case also with the single brood of *E. pissodis* Gir. and *Macrorileya oecanthi*. The number of generations each year is dependent upon the hosts attacked, and for this reason the majority of species have only a single annual generation. *E. monemae*, however, has three generations to the two of the host, and *E. oophaga* and *A. inopinata* may have a partial second which, in the latter species, is on a different host.

IMMATURE STAGES

There is a considerable degree of uniformity in the eggs of the known species of the family. In the majority of cases, the egg is oblong in form with a more or less collapsed stalk at the anterior end and a flagellum of varying length at the opposite end.

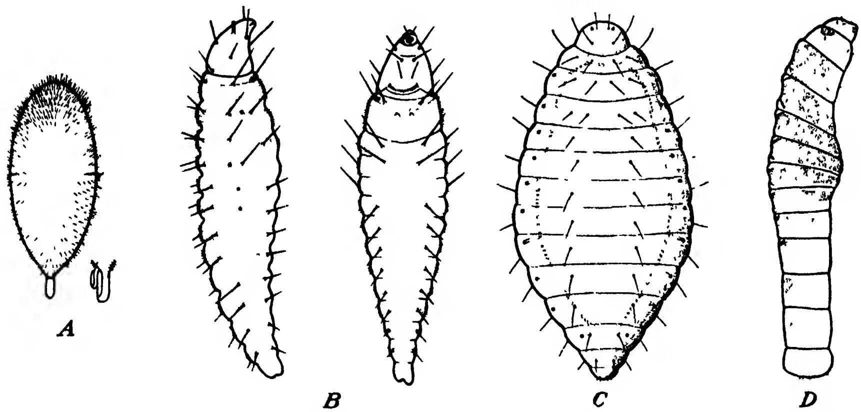


FIG. 89.—Immature stages of the Eurytomidae. *A*, the egg of *Eurytoma tylodermatis* Ashm. (*from Pierce et al.*, 1912); *B*, the first-instar larva of *E. rosae* Nees, lateral and ventral views (*from Parker*, 1924); *C*, mature larva of *E. masii* Russo (*from Russo*, 1938); *D*, mature larva *Archirileya inopinata* Silv. (*from Silvestri*, 1920).

The stalk may range in length from half that of the egg body to five or six times its length, as occurs in *Macrorileya oecanthi*. In this species, the stalk is much more slender than usual, being virtually a filament. In some species, the posterior flagellum is greatly reduced or lacking. In the externally deposited eggs of *Eurytoma*, the chorion exhibits a distinct sculpturing which, in *E. pissodis* Gir., is described as a black pubescence, whereas in others it is stated to consist of short but strong "spines" (Fig. 89*A*). These spines are densely placed and give the egg a color ranging from brownish to black. The stalk and flagellum lack this sculpturing. The ovarian egg of *E. oophaga* Silv. has reticulate markings on the chorion; after deposition, this sculpturing is in the form of fine spines. The egg of *E. curta* is cylindrical and measures 0.4 by 0.07 mm.; the stalk is 1.1 mm. in length, and the chorion is unsculptured. Eggs of *Macrorileya* and *Archirileya* likewise lack the surface sculpturing.

The first-instar larvae of the family are broadly oval to elongate in form, with 13 distinct body segments and a relatively large, hemispherical or conical head. The head bears a number of sensory setae which, in *E. appendigaster*, are very large. The sensory setae, of which there are four pairs on each thoracic segment and three on the abdomen, may be minute, as in *E. curta*, or may exceed the length of a segment, as

in *E. robusta* and *E. parva*. The integumentary setae are abundant in *Eurytoma* and may completely clothe the body or occur as a band on each segment. The larva of *A. inopinata* is apparently devoid of setae. In *E. rosae* Nees (Fig. 89*B*) and *E. parva*, a pair of small, sclerotized processes of unknown function is found on the venter near the median line of the first thoracic segment. The normal equipment of spiracles in the family is four pairs, situated on the mesothorax and the first three abdominal segments. *E. parva* has five pairs, the additional one being on the metathorax. *E. curta* is provided with 10 pairs, on the second and third thoracic and the first eight abdominal segments. *A. inopinata* has eight pairs, situated on the mesothorax and the first seven abdominal segments.

The second-instar larva has been described for only a few species; it differs from the preceding instar mainly in the reduction of the sensory setae. *E. oophaga* still has the four pairs of spiracles situated as in the first instar; in *E. parva* the number is increased from five to nine and in *A. inopinata* from eight to nine. They are situated on the last two thoracic and the first seven abdominal segments. *E. dentata* Mayr has eight pairs, that on the second thoracic segment being lacking.

Five larval instars have been distinguished in a number of species, and this is presumably the normal number for the family, though only four are indicated for *E. oophaga*. In this species, the full complement of nine pairs of spiracles appears first in the third instar.

The mature larva of *Eurytoma* is more robust than the preceding instars. The sensory setae are usually small, though they are relatively long in *E. dentata* and *E. masii* Russo (Fig. 89*C*). Cuticular spines are minute or lacking. The larvae of *Archirileya* (Fig. 89*D*) and *Macrorileya* differ markedly from those of *Eurytoma*, being cylindrical, with the caudal segments broad and the last one broader than those preceding it and forming a disk or sucker. There are 12 apparent body segments rather than the usual 13, and the anterior ventral region of the abdomen is appreciably distended. Intersegmental welts occur dorsally from the first thoracic to the sixth abdominal segments. The larvae of *Axima* and *Conoaxima* have large median dorsal welts on the thoracic and the anterior abdominal segments. The nine pairs of spiracles, on the second and third thoracic and the first seven abdominal segments, occur in all genera, though *E. curta* is stated to have an additional vestigial pair on the eighth abdominal segment.

MISCOGASTERIDAE

This is a small family of which the host preferences of only a few species are known. The species of *Scutellista*, *Tomocera*, *Aphobetoideus*, and *Anysis* are essentially predators upon the eggs of lecaniine Coccidae. *Miscogaster* is known as an internal parasite of the larvae of leaf-mining Agromyzidae, while *Megorismus* is parasitic in Aphididae, and several genera are recorded from hymenopterous hosts. Several species of *Dinarmus* have been recorded as solitary external parasites of the larvae of Trypetidae. The host preferences of the family appear to be varied, and the host relationships cover a wide range, extending from predatism upon the eggs and larvae of other insects to true internal and external parasitism. The family appears to be most closely related in habit to the Pteromalidae.

The single representative of the family that has been utilized extensively in biological control work is *Scutellista cyanea* Motsch., which was

originally introduced from Italy to Louisiana in 1898 against *Ceroplastes* and from South Africa to California in 1901 for the control of the black scale, *Saissetia oleae* Bern. It became established and in some sections infested an exceedingly high percentage of the scales, but this often resulted in very little appreciable reduction in the host population, owing to the fact that the parasite larva does not consume the entire quota of eggs beneath the host and consequently a sufficient number remains thoroughly to infest the trees. Also, in California it has largely replaced *Tomocera californica* How., a species of similar habit, which previously had effected approximately the same limited degree of control.

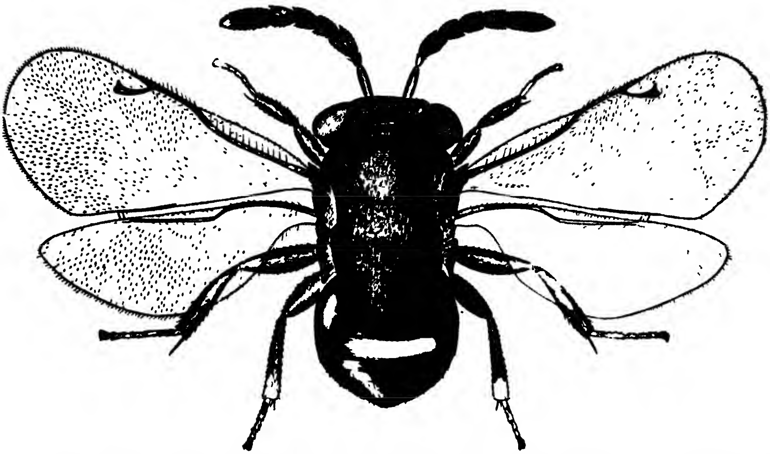


FIG. 90.—The adult male of *Scutellista cyanea* Motsch. (*From Smith and Compere*, 1928.)

BIOLOGY AND HABITS

S. cyanea (Silvestri *et al.*, 1908; Smith and Compere, 1928) is predaceous upon the eggs of various lecaniine Coccidae contained in the cell beneath the body of the parent female. If eggs are not available, the larva is able to develop in the role of an external parasite of the female scale. The preferred hosts are *Saissetia oleae* and *Ceroplastes rusci* L., though it has been recorded occasionally from several other genera, including *Coccus* and *Phenacoccus*.

In selecting hosts for oviposition, the female shows a marked preference for mature females, usually those which have just deposited a portion or all of their eggs. The scale is first examined carefully with the antennae until the posterior arch is found, whereupon the position is reversed and the ovipositor inserted by a backward thrust through the arch. At times, eggs are laid under scales from which all the young have already emerged and also under those which have just completed the second molt and consequently have laid no eggs whatever. Under

normal conditions, the parasite eggs are found among those of the host; they may be readily distinguished by their larger size and white color, in contrast to the pinkish tinge of the host eggs. If no host eggs are present, the parasite egg adheres to the venter of the scale body.

Immediately after hatching, the young larva begins its feeding upon the host eggs. When maturity is reached, a pupation cell is formed among the mass of empty eggshells and debris. This debris is matted together with a small amount of silk, of which strands are also used to bind the inner edge of the scale to the substratum. The meconium is then cast, and pupation takes place. At emergence, the adult cuts a circular opening in the dorsum of the dead host, similar to though larger than those of the true internal parasites. It has been noted that the old parasitized scales adhere closely and remain on the tree much longer than those not parasitized. They may persist *in situ* for two or three years.

The life cycle from egg to adult covers a period of about 41 days, of which 4 to 6 days are required for incubation of the egg, 15 to 21 days for the larval stage, and 15 to 20 days in the pupal stage. The newly transformed adult may remain under the scale for several days before emerging.

The seasonal cycle of *Scutellista* is correlated with that of the host. In the sections of California in which the host has a distinct annual cycle, the parasites are abundant only during June and July, for there is no suitable alternate host available in sufficient numbers to maintain a high population. Optimum conditions for the parasite necessitate a continuous supply of maturing scales, and this condition is approached only in the coastal sections. There is no definite hibernation stage in California, and development continues, though at a much reduced rate, throughout the winter. In Italy, there are about five generations each year, the first being upon *Ceroplastes* and the remaining four upon that genus, *Saissetia*, and *Philippia*.

In the case of small *Saissetia* females, which produce in the neighborhood of 500 eggs, a single parasite larva is able to consume the entire lot, and it thus completely prevents reproduction. Large scales, however, may deposit 2,500 or more eggs, and only a portion of these can be eaten by a single larva. The control effected is thus considerably greater upon small than upon large hosts.

The recent observations by Gurney and Compere upon *Scutellista cyanea* attacking *Ceroplastes* and *Saissetia* indicate that these are distinct biological forms, which are not readily transferable from one host to the other. In Australia, the parasite attacks only *Ceroplastes*, whereas the African form is upon *Saissetia*. The first introduction into the United States was of the wax-scale form from Italy to Louisiana, whereas the

California introductions were of the black-scale form from South Africa. It may be mentioned that both hosts are heavily attacked in Italy, though no studies have been made to determine the existence of distinct forms upon them.

The habits of other coccid-infesting species of the family are similar to those of *Scutellista cyanea*. *Tomocera californica* (Smith and Compere, 1928) on the same host oviposits at times through the posterior arch and at other times around the periphery of the scale. Like *Scutellista*, also, the larva is able to develop as an external parasite of the female scale if eggs are not available. *Aphobetoideus comperei* Ashm. inserts the ovipositor beneath the lateral margin.

An undetermined species of *Miscogaster* observed in France by Parker and Thompson (1925) develops as a solitary internal parasite of the larvae of *Agromyza* mining the leaves of alfalfa. The ovipositor is inserted through the surface of the leaf and into the body cavity of the host. The tip of the egg stalk remains fixed in the puncture in the host integument, but the larva does not maintain a connection with it after hatching.

Ahmad and Mani (1939) have observed the habits of the immature stages of *Systasis dasyneurae* Mani, which differ in several respects from those of other members of the family. The larvae are predaceous upon the second-instar larvae of the midge, *Dasyneura lini* Barnes, in the buds of linseed in India.

The eggs are deposited singly within the crumpled and unopened flower buds containing well-developed midge larvae, though not necessarily in their immediate vicinity. The newly hatched larva is very active and usually finds the midge larvae within a short time. Three or four of these, the usual population of an infested bud, are required to bring the predator to maturity; but if a greater number is present all are killed, though they are not completely eaten. Pupation takes place within the bud. The cycle from egg to adult is complete in 25 to 32 days at 18°C.

IMMATURE STAGES

The ovarian eggs of the Miscogasteridae are of the two-bodied type, but at deposition the anterior body disappears and only a stalk or peduncle remains. In *Scutellista* (Fig. 91*A*), *Miscogaster*, and *Anysis*, this stalk or peduncle is about half the length of the egg body; but in *Aphobetoideus* (Fig. 91*B*) it is broad and stub-like and in *Tomocera* nipple-like and minute. The egg of *Dinarmus dacicida* Masi is ovate in form and lacks either a stalk or a peduncle.

The first-instar larvae are hymenopteriform, with a variable number and arrangement of segmental spines. That of *S. cyanea* (Fig. 91*C*) bears no spines whatever, whereas *Miscogaster* sp. (Fig. 91*D*) has a complete ring of 30 to 40 heavy spines about each segment. In *T. californica*, there are only two pairs on each segment, whereas in *Systasis dasyneurae* three rows encircle each segment. Spiracles are found on the

second and third thoracic and the second and third abdominal segments in *Scutellista cyanea*, on the second thoracic and first three abdominal segments in *Anysis saissetiae*, and on the second thoracic and first and fifth abdominal segments in *T. californica*. No spiracles are described or figured for *Miscogaster* sp., which is further distinguished from others of the family by the bilobed form of the last abdominal segment, each lobe terminating in a heavy spine.

The intermediate-instar larvae have not been described for any species, nor has the number of stages been determined.

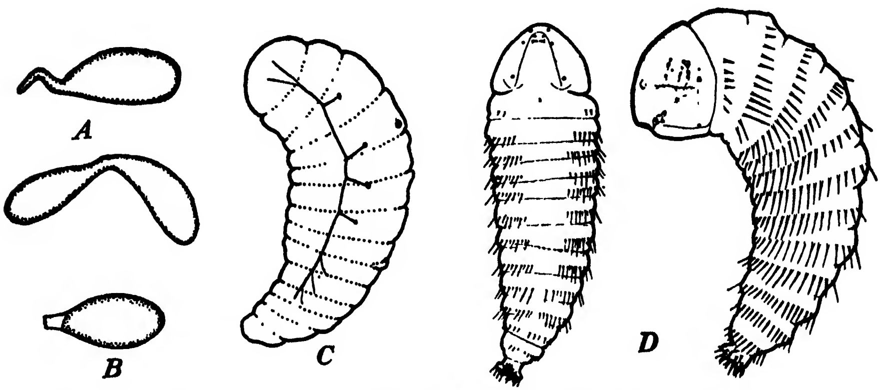


Fig. 91.—Immature stages of the Miscogasteridae. *A*, Ovarian (below) and laid egg of *Scutellista cyanea* Motsch.; *B*, laid egg of *Aphobetoideus comperei* Ashm.; *C*, first-instar larva of *S. cyanea* (*from Smith and Compere*, 1928); *D*, first-instar larva of *Miscogaster* sp., ventral and lateral views (*from Parker and Thompson*, 1925.)

The mature larva has been described only for *S. cyanea*. The cuticular spines are minute or lacking and the respiratory system now possesses nine pairs of spiracles, situated on the last two thoracic and the first seven abdominal segments.

PERILAMPIDAE

The Perilampidae, excluding the phytophagous forms that are questionably placed in the family, are encountered mainly as hyperparasites of Lepidoptera through a variety of dipterous and hymenopterous species. The host preferences of *Perilampus* only are known, and these have been summarized by H. S. Smith (1912). In addition to the records as a hyperparasite, a number of species of the genus are listed as primary parasites of Lepidoptera, Coleoptera, Hymenoptera, and Neuroptera. It is quite certain, however, that many of such records are open to question, though Boselli (1932) has apparently established that *P. italicus* F. is a true external parasite of the larva of *Athalia colibri* Chr. in the cocoon and Smith (1917) has shown that *P. chrysopae* Cwf. develops as an external parasite of the pupa of *Chrysopa* in its cocoon. In view of these findings, it is quite possible that some of the records of direct parasitization of wood-boring Coleoptera and gall-making and stem-infesting Lepidoptera may prove to be correct.

BIOLOGY AND HABITS

The only extensive accounts that have been published upon the Perilampidae are those by Smith (1912) upon *Perilampus hyalinus* Say and by Bergold and Ripper (1937) upon *P. tristis* Mayr. The first is an indirect parasite of *Hyphantria textor* Harr., through *Ernestia ampelus* Wlk. (given as *Varichaeta aldrichi* Tns.) and other dipterous and hymenopterous parasites; the second has the same relationship to the European pine-shoot moth, *Ryacionia buoliana* Schiff., through its various ichneumonid and tachinid primary parasites. D. W. Clancy has recently completed a study of the biology and habits of *P. chrysopae*, an account of which is now in press; the author is indebted to him for permission to use some of his material for the following summary of its habits and several of his illustrations of the different instars.

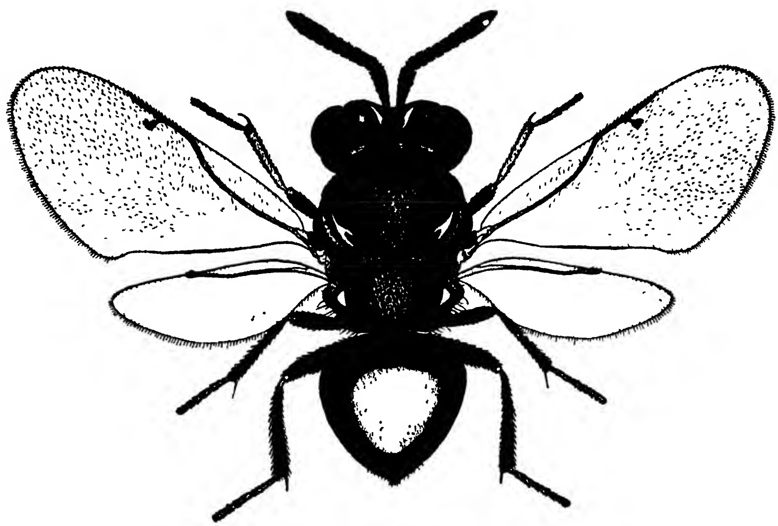


Fig. 92.—The adult female of *Perilampus chrysopae* Cwf. (*Drawing by D. W. Clancy.*)

Habits of the Adult.—The adult wasps are frequently found at flowers, particularly those of the Compositae, and upon aphid-infested foliage, where they apparently feed upon the honeydew. The female of *P. italicus* punctures the epidermis of the leaf with the ovipositor in order to feed upon the sap which exudes from the wound. In confinement feeding takes place readily and extensively upon sugar solutions.

The manner and place of deposition of the eggs of *P. hyalinus* were not determined by Smith, though it was surmised that this takes place upon the food plant in the general vicinity of a colony of caterpillars. Oviposition was first actually observed by him in *P. chrysopae*. The

females of this species hovered over the foliage of oleander infested with *Aphis nerii* Kalt. upon which *Chrysopa* larvae were feeding. They were noted to touch the leaf surface with the abdomen at intervals, and it was found that the eggs were deposited at these times. The eggs are lightly attached to the leaf by the posterior end. Clancy found that the aphids and mealybugs, rather than the *Chrysopa* larvae themselves, provide the stimulus for oviposition.

Boselli records a modification in the oviposition habit of *P. italicus* wherein the eggs are partially embedded individually in incisions in the epidermis of the leaf. These incisions are made in series at intervals of 20 to 40 seconds. Parker (1924) obtained oviposition of *P. tristis* upon the upper sides of the leaves of oak under insectary conditions.

The reproductive capacity of the females is relatively high, though not at all comparable to that of the related Eucharidae. A female of *P. chrysopae* deposited 52 eggs in one day, and Clancy states the total production ranges from 200 to 500. Bergold and Ripper found that the females of *P. tristis* have 56 to 94 ovarioles in the reproductive system and that each of these contains three or four mature eggs. The total available for deposition at one time is consequently several hundred. Smith found approximately 250 mature eggs in the ovaries of gravid females of *P. hyalinus*. A relatively long gestation period is indicated by the complete absence of eggs in newly emerged females.

Egg and Larval Development.—Hatching of the eggs of *P. chrysopae* takes place in four to six days under high summer temperatures; in the case of *P. italicus*, it requires 14 to 15 days at fluctuating temperatures between 16 and 38°C.

The planidium, upon emergence from the egg, undergoes a free-living period during which it must find its host. In the Perilampidae and Eucharidae, this is more exactly a waiting rather than a searching period; for relatively little movement takes place, and the greater portion of the time is passed in the erect position awaiting the arrival of a host or carrier. *P. chrysopae* planidia have been kept alive as long as 17 days without food and during this time did not change their positions. In the field, they are often found attached to the egg stalks of *Chrysopa;* this position gives them an excellent opportunity to transfer to the newly hatched first-instar host as it descends the stalk to begin its search for food. In general, the instincts of the planidium are not sufficiently developed to enable it to select a proper host, but it responds to virtually any moving object that approaches its immediate vicinity.

In the species that develop as primary external parasites, such as *P. chrysopae*, the planidium attaches itself to the host at any stage of larval development and is apparently able to effect successful transfer at the successive molts. No appreciable feeding takes place so long as

the host is in the larval stage, and the latter spins its cocoon and pupates normally.

According to Clancy, the normal host of *P. chrysopae* is *C. californica* Coq.; it is unable to develop to maturity upon *C. majescula* Banks, which is present in the same localities. In spite of this, the planidia attach themselves to the larvae of the latter species, and instances were noted where they survived upon them for five to six months; but development did not progress beyond this stage.

The stimulus that is responsible for the initiation of rapid feeding and growth is undoubtedly the histolytic changes taking place in the host body incident to pupation. The host pupa becomes inactivated during either the late first or the second larval stage of the parasite, and paralysis is accompanied by a reduction in the amplitude and rate of the heart beat. This is probably induced by the injection of some toxic glandular substance into the body.

The habits of *P. italicus* as a solitary external parasite of *A. colibri*, as reported by Boselli, are essentially the same as those of *P. chrysopae*, though the host does not attain the pupal stage.

The interrelations between *Perilampus* and its hosts are strikingly different where development is in the secondary role upon various ichneumonid, braconid, and tachinid species which are themselves primary internal parasites of caterpillars and sawflies. Smith's account of *P. hyalinus*, which was the first study of a member of the family, deals largely with its relationship to the tachinid, *Ernestia ampelus*. This fly deposits living maggots upon the foliage in the vicinity of colonies of *Hyphantria* caterpillars, and they penetrate the skin and enter the body cavity of the latter at the first opportunity. The planidia of *Perilampus* are likewise free-living on the foliage at the same time and enter the caterpillar body in the same way. Although the possibility of direct entry of the *Perilampus* planidium into the first-instar larva of *Ernestia* while it is still upon the foliage has not been investigated, yet its relative size and occurrence simultaneously upon foliage in the vicinity of colonies of caterpillars would permit direct parasitization.

The planidium of *Perilampus* that enters the caterpillar body searches about for the larva of a primary parasite, in this case *Ernestia*, which is entered in turn; there it remains, apparently without feeding, until the maggot reaches maturity, leaves the caterpillar, and pupates in the soil during the late summer or early autumn months. Immediately after the formation of the puparium, the planidium emerges from the body and takes up an external position upon the pupa. It remains in this position, apparently without feeding, throughout the winter.

With the return of warm weather in the spring, the planidium begins feeding; as growth progresses, the segmental bands become widely

separated and conspicuous against the otherwise white background of the body contents, which are revealed through the transparent intersegmental membranes. At a constant temperature of 25.5°C., the first molt takes place about 6 days after the beginning of feeding, and larval maturity is completed in a total of about 17 days, which is followed by a pupal period of 10 days.

The effect of parasitism by the minute planidium upon the tachinid pupa is conspicuous and out of proportion to the mechanical injury inflicted at emergence or to the very small amount of fluids abstracted from the body. The pupa takes on a distinctive translucent appearance, expecially in the head and thoracic regions, the head attains only half its normal size, and the eyes and appendages are only slightly developed. Thompson (1915) expresses the opinion that the minute emergence wound at this critical time brings about an upset in the equilibrium of the body fluids, resulting in virtually complete cessation of development.

When parasitic upon *Eulimneria valida* Cress., an ichneumonid parasite of *Hyphantria, Perilampus* adapts itself to the changed conditions and persists internally in the mature larva throughout the winter. Emergence and external feeding take place only after *Eulimneria* begins its transformation to the pupal stage in the spring.

Bergold and Ripper have found that the habits of *P. tristis* differ appreciably from those given above for *P. hyalinus.* This species is parasitic upon a number of species of Ichneumonidae and Braconidae which are internal parasites of the larvae and pupae of *Rhyacionia buoliana.* This moth has a single generation each year and passes the winter in the half-grown larval stage in the shoots of pine. The planidia of *P. tristis* enter the young caterpillars during August and September and are found shortly thereafter, and throughout the winter, in the fat body or a salivary gland. When activity is resumed in the spring, they may often be found attached externally to the young larvae of the primary parasites; but they shortly enter the body cavity and await the attainment of the pupal stage, which occurs during June. They then become ectoparasitic and complete their development in approximately one month.

The Life Cycle.—In the Perilampidae, the duration of the cycle from egg to adult is dependent upon the stage of the host to which the planidium attaches itself and, among the hyperparasitic species, upon the time required for the primary host to reach the pupal stage. *P. hyalinus*, as a parasite of *Ernestia,* has a single generation each year, as does *P. tristis* in the various species that attack the pine-shoot moth. In both these species, the winter and a large portion of the year are passed as an inactive first-instar larva. Smith expresses the opinion that *Perilampus*, when developing as a parasite of summer-issuing Tachinidae, attains the

adult stage in the autumn and hibernates as such within the host cocoon or puparium. The European *P. cuprinus* Foerst. has this habit. It is probable that the above species produce several generations each year upon multibrooded hosts.

According to Clancy, *P. chrysopae* is able to complete its cycle in a minimum of 18 days, of which the egg, larval, and pupal stages require 4, 8, and 6 days, respectively. This very short cycle is made possible by direct attack upon a host that also has a short cycle and is initially attacked in its mature larval stage. The winter is passed in the pupal stage.

IMMATURE STAGES

The egg of *P. chrysopae* (Fig. 93) is subcylindrical and distinctly arched on one side, with one end rather sharply pointed and the other bearing a short, broad peduncle. It is pearly-white in color, and the chorion is characteristically sculptured, with irregular elongate areas that extend lengthwise. The eggs of *P. tristis* (Fig. 93) and *P. italicus* are very similar. The size of these eggs, which measure 0.25 mm. in length in *P. chrysopae* and 0.41 mm. in *P. italicus*, contrasts strongly with the very minute stalked eggs of the related Eucharidae.

The first-instar larvae of *Perilampus* are all of the planidium type, with heavy segmental bands that almost reach the median ventral line. There are 13 body segments, of which the first 12 bear the sclerotized bands and the thirteenth is represented by the caudal sucker. Specific differences occur in the form of the terminal portions of the bands and in the number, size, and position of the body spines and the "scales" and hooks on the membrane of the venter of the anterior portion of the body. The pleural plates, which have been distinguished upon the planidia of the Eucharidae and of families of other orders having larvae of this type, are absent or not recognizable.

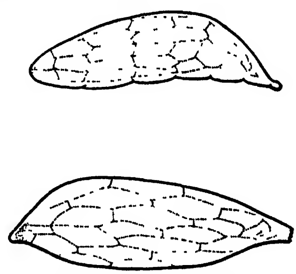


FIG. 93.—The eggs of *Perilampus tristis* Mayr (above) (*from Parker*, 1924); and *P. chrysopae* Cwf. (below) (*from Smith*, 1917).

On the larvae of *P. hyalinus* (Fig. 94*A*) and several others, the posterior margins of the terminal portions of each band bear numerous sharp teeth, whereas in *P. chrysopae* (Fig. 94*B*) they are smooth. The sensory spines are exceptionally long and heavy in the latter species. The two caudal cerci arise dorsolaterally from the last segmental band. In *Perilampus* sp. from *Conocephalus* (Ford, 1922), they are approximately half the length of the body.

Spiracles have been detected in *P. hyalinus*, *P. chrysopae*, *P. tristis*, and several undetermined species; all these except the first have a single pair dorsolaterally at the anterior margin of the band of the second thoracic segment or on the membrane between the first and second segments. In *P. hyalinus*, the spiracles are on the intersegmental membrane but distinctly ventral.

The number of larval instars is uncertain. Smith recognized only three in *P. hyalinus*, whereas Parker describes four for the same species and Bergold and Ripper found the same number in *P. tristis*.

The second-instar larva of *P. hyalinus* (Fig. 95*B*) lacks the specialized characters of the first instar, and the body is white and distinctly segmented. The sensory setae

are small and set upon tubercles, and each segment bears a band of minute integumentary setae at the anterior margin. The two pairs of large spiracles are situated on the mesothorax and the first abdominal segment. The larva of *P. chrysopae* (Fig. 95*A*) is similar, though more robust, but in *P. tristis* the spiracles are said to be on the pro- and metathorax.

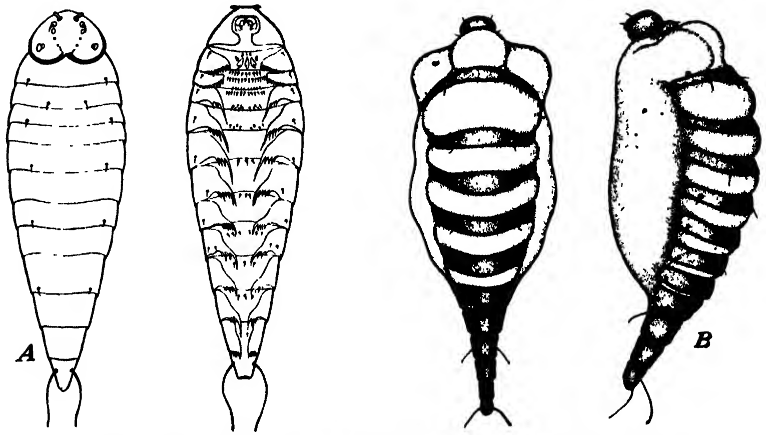


FIG. 94.—First-instar larvae of *Perilampus*. *A*, *P. hyalinus* Say, dorsal and ventral views (*from Smith*, 1912); *B*, *P. chrysopae* Cwf., dorsal and lateral views, after extensive feeding (*drawings by D. W. Clancy*).

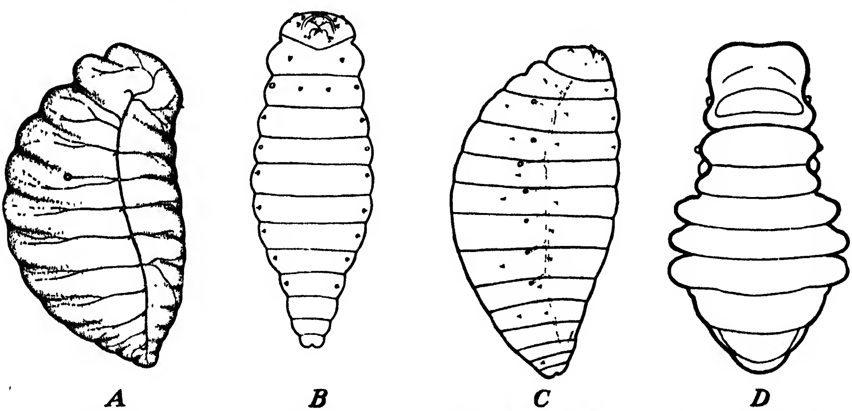


FIG. 95.—Immature stages of the Perilampidae. *A*, the second-instar larva of *Perilampus chrysopae* Cwf. (*drawing by D. W. Clancy*), *B* and *C*, second- and third-instar larvae of *P. hyalinus* Say (*from Parker*, 1924); *D*, mature larva of same (*from Smith*, 1912).

The third-instar larva of *P. hyalinus* (Fig. 95*C*) is rather indistinctly segmented but still bears the sensory and integumentary setae mentioned for the second instar. There are now seven pairs of spiracles, situated on the last two thoracic and the first five abdominal segments, of which the first and third are largest. In *P. tristis*, the number and position are the same.

The fourth-instar larva of *P. hyalinus* (Fig. 95*D*), which is the mature form, is of distinctive form, being very robust and bent ventrally in the thoracic region, with large

lateral segmental "bosses" on the first five abdominal segments and distinct fleshy tubercles of testaceous color at the lateral margins of the second and third thoracic segments. The sensory and integumentary setae of the preceding instars persist. There are nine pairs of spiracles, the additional two pairs being on the sixth and seventh abdominal segments. The larva of *P. tristis* is similar except that the thoracic tubercles occur on all three segments.

The pupae of the different species are short and robust, with the abdomen almost spherical and bearing transverse intersegmental welts similar to those of some Eucharidae.

EUCHARIDAE

The family Eucharidae is a homogeneous group, closely related to the Perilampidae, in which the adults are frequently of large size and brilliant metallic blue or green in color, with some species showing conspicuous modifications in the form of the scutellum, represented by a bifurcate process, the prongs of which may extend to the end of the abdomen. The host preferences of the members of the family are remarkably consistent, and all species of which the hosts are known are parasitic upon the mature larvae or pupae of ants. The genus *Orasema* appears to be most frequently associated with *Pheidole* and *Solenopsis*, *Stilbula* with *Camponotus*, *Eucharis* with *Formica*, and *Kapala* with *Odontomachus*. The records, however, are as yet too few to permit of any accurate statement regarding the host preferences of any of the genera.

The first studies on the biology of the family were those by W. M. Wheeler (1907) on *Orasema viridis* Ashm. and other species of genus. These and later investigations by various workers led to the conclusion that all species were probably ectoparasitic, but recent observations have shown that two species of *Orasema* develop internally, at least during the early stages.

BIOLOGY AND HABITS

Since the early observations upon *Orasema* by Wheeler, the more important contributions to our knowledge of the family have been those of Clausen (1923, '28*a*), Ishii (1932*b*), H. L. Parker (1932, '37), and Wheeler and Wheeler (1937). To these the author is now able to add new information relating to a number of additional genera and species.

Habits of the Adult.—The mating habits have been observed in some detail only in *Schizaspidia tenuicornis* Ashm. (Clausen, 1923) and *Kapala terminalis* Ashm. In both species, this takes place immediately after emergence from the ant nest. On bright sunshiny days, swarms of males of *Schizaspidia*, often comprising 100 or more individuals, may be observed hovering 1 or 2 ft. above the entrance of the *Camponotus* nest from 9:00 A.M. onward. As soon as a female appears, she is pounced upon and mating is soon accomplished. This swarming of the males

above the entrance to the host nest appears to be a general habit in many species of the family and provides one means by which the host may be quickly determined and the immature stages secured. The males of *Kapala* rest quietly upon the foliage near the nest entrance and await the emergence of the females. Mating takes place as soon as the latter settle upon the near-by leaves. W. M. Mann (Wheeler, 1928) observed several males of *Orasema* sp. in the act of mating with female pupae in the ant nest.

The adults of the majority of species do not require food. This applies particularly to those which deposit their eggs en masse; for the eggs are all fully developed at the time of emergence of the females, and

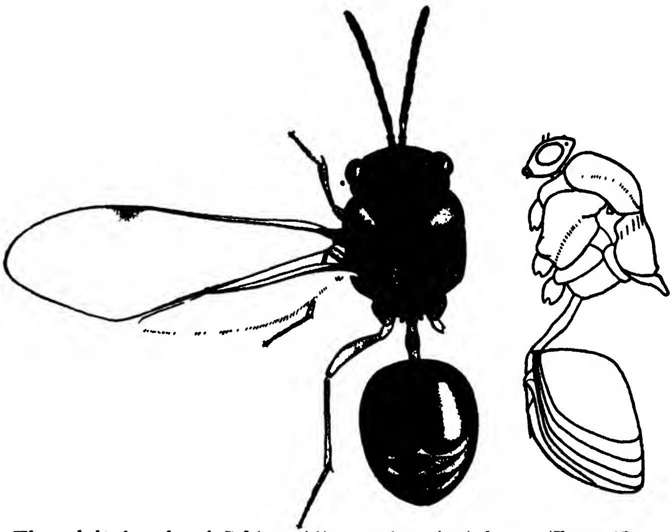


FIG. 96.—The adult female of *Schizaspidia tenuicornis* Ashm. (*From Clausen,* 1923.)

oviposition is completed in one or two days. Other species, which have a more extended oviposition period, probably partake of food, and *K. furcata* F. has been seen to imbibe honeydew secreted by aphids. Wheeler mentions that the adults of *O. viridis* are fed with regurgitated material by the worker ants.

Oviposition.—For many years, entomologists speculated upon the probable manner of oviposition in this family; but, strangely enough, the clue was finally found purely by accident in connection with observations upon other subjects. Pierce and Morrill (1914), in their survey of the insects infesting wild cotton in Arizona, observed two females of *Chalcura arizonensis* Cwf. with their ovipositors inserted in apparently healthy squares. The females and squares were placed in vials without being disturbed, and the squares, upon later examination, revealed compact

masses of eggs at the points of insertion of the ovipositors. This record was entirely overlooked by following workers upon the family, and it was not until some years later that the same oviposition habit was observed in another species. Once the key to the problem became generally known, the habits of a considerable number of species were determined. In every instance, egg deposition has been found to be entirely apart from the ant host, and a surprising range of adaptations in oviposition habits has been revealed.

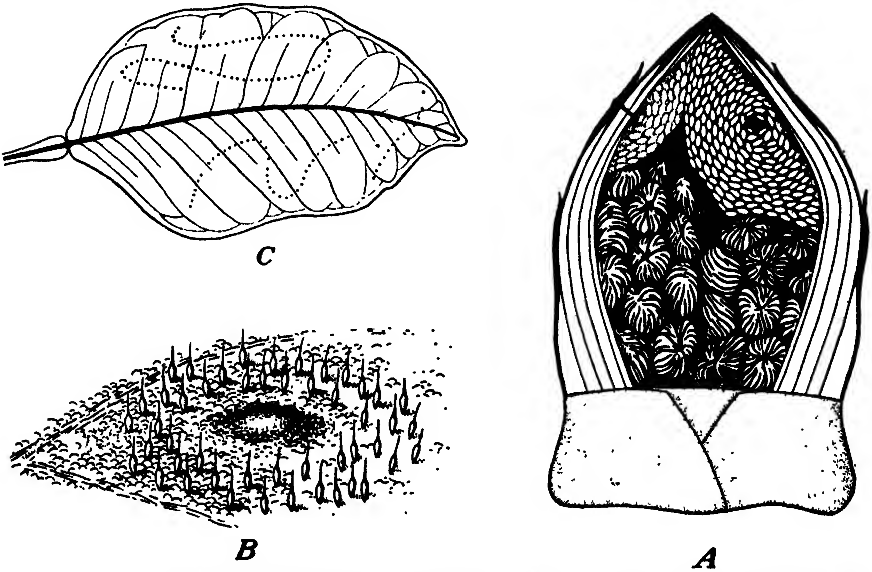


FIG. 97.—Oviposition habits of the Eucharidae. *A*, two egg masses of *Schizaspidia tenuicornis* Ashm. within a mulberry bud (*from Clausen*, 1923); *B*, a cluster of eggs of *Psilogaster* sp. on the leaf surface about an egg of *Selenothrips rubrocinctus* Giard; *C*, serpentine lines of oviposition punctures of *Schizaspidia* sp. on the under side of a fleshy leaf. Each incision contains one to five eggs (original).

In all the species thus far studied, representing nine genera and 17 species, there is a direct association of oviposition with some plant, whereas there is none with the host itself. The discussion that follows will be on the basis of the manner of oviposition and the part of the plant in or on which the eggs are deposited.

1. *In Overwintering Buds.*—The female of *S. tenuicornis* selects for oviposition certain nonresinous trees that have rather loosely packed buds. Those preferred in northern Japan are wild mulberry and chestnut. Immediately after emergence and mating, the female ascends to a suitable tree, inserts the ovipositor through the bud scales into the central cavity, and deposits her entire quota of eggs en masse (Fig. 97*A*) within a period of about 20 minutes. A considerable number of these

masses may be found in each bud, and where this is excessive the pressure exerted by the last individuals to utilize the bud is sufficient to force a ribbon of eggs out between the scales or through earlier oviposition punctures. One mulberry bush 7 ft. high was estimated to contain an average of more than seven masses per bud, or a total of approximately four million eggs (Clausen, 1923).

2. *In Expanding Leaf and Flower Buds.*—*Eucharis* sp. of Chosen (Korea) places its egg masses in expanding or fully opened flower buds of *Cebata orbicula* Kunz. These flowering plants have a remarkable attraction for the female *Eucharis;* a sprig held over the entrance to the host nest will attract all the females in the vicinity within five minutes, and they will cling to it tenaciously. *Kapala furcata* F. oviposits in the expanding flower buds of *Mikania micrantha* H.B.K. and an undetermined species of Amaranthaceae in Panama. Only a few eggs are placed in each bud, and the female moves frequently from bud to bud. *S. manipurensis* Clausen places its large egg mass beneath the outer scales of the loose buds of *Flamingia latifolia* var. *grandiflora. S. convergens* Wlk. and *Chalcura deprivata* Wlk. of Ceylon do likewise in the buds of the jak fruit, *Artocarpus integrifolia,* and the latter species also utilizes the flower buds of croton and *Cordia myxa.*

3. *In Seed Pods.*—The only species known to utilize the seed pods rather than leaf or flower buds is *Stilbula cynipiformis* Rossi, which oviposits in the pods of a small composite plant, *Picris hieracioides* var. *spinulosa* Gussone (H. L. Parker, 1937). The eggs are freed a few days later by the opening of the seed pod, and the egg masses are usually found to adhere to the seed, which are provided with plumes to facilitate dispersion by wind.

4. *At Random on the Leaf Surface.*—*K. terminalis* Ashm. of Cuba consistently deposits its eggs at random on the under sides of the leaves of *Tragia volubilis* L. One female in captivity deposited approximately 10,000 eggs in six hours. Leaves seen in the field were so heavily covered with eggs as to appear overgrown with a fungous mycelium. Ishii (1932*b*) records the same habit in *Parapsilogaster montanus* Gir.

5. *In Incisions in Leaf Tissue.*—This habit occurs in several genera, and its distinguishing feature is that only one to six eggs, depending on the species, are placed in each incision. Fleshy leaves, in which a small cavity is formed by drying out when the epidermis is punctured, are most suitable for oviposition. *Schizaspidia* sp. of Malaya favors the large leaves of *Eugenia* and *Medinella,* though occasionally it oviposits in the fleshy stems of the blossom clusters. The incisions are spaced about 1.0 mm. apart and in distinctly serpentine rows (Fig. 97*C*). The tissue surrounding the puncture dies and becomes black, resulting in a conspicuous marking of the leaf. *Parapsilogaster* sp. of Ceylon oviposits

likewise in the half-grown leaves of jak fruit, though the incisions are not in serpentine lines. *Kapala* sp. and *Orasema smithi* How. make incisions in the leaves of *Tragia* and *Casearia*, and *O. coloradensis* oviposits in those of *Stylosanthes biflora* in Virginia. Ishii mentions the same habit for *K. foveatella* Gir. and *Losbanos uichancoi* Ishii in the Philippine islands, and the incisions of the latter species are stated to be in two short parallel rows.

6. *Upon Leaf Surface Associated with Thrips Eggs.*—This is the most remarkable of the adaptations for oviposition found in the family, and the relationship appears to be obligatory. The females of a species of *Psilogaster* observed in Malaya occur commonly on mango and other foliage infested with *Selenothrips rubrocinctus* Giard. This thrips embeds its eggs singly in the leaf tissue and covers them with a mass of excrement. The *Psilogaster* female deposits her eggs, standing vertically and evenly spaced, in clusters of 50 to 100 or more, surrounding a freshly laid thrips egg (Fig. 97*B*). It was not possible to secure oviposition in the absence of these eggs, and no clue has yet been found in explanation of this association.

Even the incomplete discussion of the oviposition habits of the family given above illustrates the remarkable range in adaptation that has been developed, and further investigations will undoubtedly bring still other habits to light. With the host preferences so consistent, it is surprising that such diverse oviposition habits should have been developed.

The reproductive capacity of all species is high, ranging from approximately 1,000 in *Schizaspidia tenuicornis* and a number of others to 10,000 to 15,000 in *K. terminalis* and *Stilbula cynipiformis*. Those with the higher reproductive capacities almost invariably deposit the entire quota in one or at most two days. This high capacity is essential to the survival of the species in view of the hazards encountered during the early stages.

Development of the Immature Stages. *Incubation of the Egg.*—*S. tenuicornis* is the only member of the family definitely known to pass the winter in the egg stage. The egg masses, with the larvae fully developed within them, remain in the plant buds from the time of deposition in late August and early September until the following spring. Those which are contained in healthy buds fall from the tree with the bud scales when they open and are presumably lost. A portion of the buds die during the winter and dry out, resulting in the scales spreading apart to a certain extent. Eggs contained in these buds normally hatch during July, and the planidia are able to escape.

The incomplete observations by Parker upon *Stilbula cynipiformis* point to the possibility of overwintering in the same stage. Oviposition takes place during August and September, and none of the egg masses hatched during the period they were under observation.

The eggs of species that oviposit in expanding flower and leaf buds or in incisions in leaf tissue or upon the leaf surface have a relatively short incubation period, ranging from 7 to 15 days.

Activities of the Planidium.—The first-instar larvae of the Eucharidae are all of the planidium type, as is understandable considering that they must undergo a protracted free-living period from the time of hatching until the host is reached. It has been pointed out that the eggs of all species are deposited in vines, shrubs, or trees, often at some distance from the ant nest, and consequently the planidia must find their way into the nest. Those of *S. tenuicornis* emerge from the buds and take up a waiting position upon the leaves and twigs near by. The foliage of these trees is infested with aphids at this season, and worker ants are present in numbers feeding upon the honeydew. The planidia attach themselves to those workers and are thus carried into the nest, where they transfer to the larvae.

In the case of several species of *Kapala*, *Schizaspidia*, and *Chalcura* that are parasitic upon *Odontomachus*, the above method of reaching the nest is impossible; for the ants of that genus, so far as observed, do not forage in trees. This difficulty is overcome by the development of the jumping habit, wherein the planidia stand erect upon the caudal sucker and, by the use of the caudal cerci, project themselves into space. They thus reach the ground, and from this point onward the course of events is the same as given for *Schizaspidia*.

A strikingly different procedure is followed by *Psilogaster* which, as already mentioned, is associated with thrips. The parasite eggs are fully incubated at the time of hatching of the thrips egg, and the young thrips, as it emerges, finds itself surrounded by the cluster of erect *Psilogaster* eggs. During the time it is clambering around among them, many of the eggs may hatch, and the planidia immediately attach themselves to the body of the thrips. One of the latter was found to bear 53 planidia, representing several times its own weight. This association is not accidental, for the planidia consistently retain their position until the first molt of the carrier. Unfortunately, the ant host of this species was not discovered, and the further details of the life history, after abandonment of the thrips carrier, could not be determined.

Stage of Host Attacked.—Upon gaining access to the ant nest, the planidia of the ectoparasitic species attach themselves to virtually any larval instar and then await its development to the prepupal or pupal stage before extended growth takes place. In *S. tenuicornis*, the first molt takes place while the host is in the prepupal stage, and it is the young second-instar larva that transfers to the pupa and takes up the feeding position in the pleural region beneath one of the wing pads or

hind legs. The host pupa is fully formed before its development is arrested by the parasite. *O. viridis,* on the other hand, kills the *Pheidole* host in its prepupal stage, while the appendages are in an incipient stage of development. The feeding position of the parasite is usually on the venter of the thorax.

The planidia of *K. terminalis* are usually found attached to the throat of the *Odontomachus* larvae, somewhat to one side. Transfer to the pupa is effected just prior to the first molt of the parasite, and the appendages of the pupa never attain more than half their full length.

The two known endoparasitic members of the family, *Orasema costaricensis* W. & W. and *O. sixaolae* W. & W., attack the larvae of *Pheidole* and *Solenopsis,* respectively (Wheeler and Wheeler, 1937). The planidia were found embedded in the host bodies, with the posterior end fixed in the entrance hole in the integument and surrounded by a "collar" strikingly similar in formation, and apparently in function, also, to the respiratory funnel of many Tachinidae. It is not known whether the second and third instars are endo- or ectoparasitic, though mature larvae were found free in the nest.

Larval and Pupal Development.—Once the prepupal or pupal stage of the host is reached, the development of the parasite larva is exceedingly rapid. Only a single feeding puncture is made, and, except in *S. tenuicornis,* the parasite is incapable of ordered movement after the first molt. The larva of *S. tenuicornis* and most other genera completely suck out the contents of the host body, whereas *O. viridis* abstracts only a portion of it. The completeness with which the pupa is emptied of its contents through the single feeding puncture suggests to Brues (1919) the occurrence of extraintestinal digestion.

The first exuviae of *S. tenuicornis* remains attached to the last larval skin of the host, whereas in the other ectoparasitic species of the family it remains adhering to the venter of the second parasite instar. The mature larvae of these species bear the two larval exuviae in leaf-like form on the mid-ventral area of the body.

Pupation takes place within the host cocoon, if one is formed, or naked in the ant nest. In emerging from a host cocoon, the eucharid adult thrusts one of its sickle-like mandibles through the envelope and then quickly cuts away the entire anterior end.

The ants exhibit no antipathy toward any of the parasite stages. They have been observed to lick the larvae and pupae of *Orasema* and to care for them much as they do for their own brood.

The Life Cycle.—The cycle of the Eucharidae is dependent upon two principal factors, one of which is climate and the other the stage of development of the host brood. In the tropics, where the ants breed

continuously, the parasites do likewise, whereas in temperate regions the species that have been studied reveal only a single generation each year, with the adults present for only a few weeks. In northern Japan, *S. tenuicornis* emerges during late August and early September, whereas in Chosen the adults may be found in late June. This variation in time of emergence is probably correlated with the cycles of the hosts, which are different subspecies, in the two sections. The winter is passed in the egg stage, and hatching takes place the following July. The egg stage thus covers about 11 months and the first larval stage a variable period up to 20 days, after which 7 days are required from the first molt to larval maturity and 6 days for the pupal stage.

Eucharis sp. attacking *Formica* in Chosen emerges during June, and the greater portion of the year is apparently passed in the inactive planidium stage upon the bodies of immature host larvae. In Virginia, *O. coloradensis* Wheeler begins emergence the first week in July, and adults may be found for a period of only three weeks. Wheeler observed the same species in Colorado during August, but he found *O. viridis* in the field in Texas during May and June and reared several broods in artificial nests during the remainder of the season. In view of what is now known of the oviposition habits of *Orasema*, it seems quite certain that these "broods" did not represent successive generations.

While the period of adult occurrence in temperate regions is very short, yet even this is much longer than the life of the individual females. Oviposition normally begins within an hour or so, often within a few minutes, after emergence from the ant nest, and in *S. tenuicornis* it is usually completed the same day, in fact within 20 to 40 minutes. Death then follows with little delay. Under caged conditions giving no opportunity for oviposition, the maximum length of life was five days. In *Orasema*, *Psilogaster*, and others, which deposit their eggs in small numbers in incisions in leaf tissue or elsewhere, adult life is prolonged and oviposition may extend over a number of days.

IMMATURE STAGES

The eggs of the Eucharidae are all of the stalked type and, because of the enormous numbers produced by each female, exceedingly minute. The egg body is ellipsoidal in form and greatly arched dorsally and ranges from 0.1 to 0.2 mm. in length in the different species. The slender anterior stalk is one-fourth the length of the egg body in *Parapsilogaster montanus* as compared to twice its length in *Psilogaster* sp. and *Stilbula cynipiformis*. At deposition, the eggs are translucent, but as incubation progresses they assume a deep amber color, with the heads of the larvae appearing almost black.

The first-instar larvae are all of the planidium type, distinguished by a large, heavily sclerotized head and heavy, segmental bands that terminate lateroventrally in pleural plates. These bands are separated by transparent membranes, which are not visible until feeding takes place, and in active individuals the successive segments telescope into those preceding. Because of this, it is difficult to determine the exact

number of body segments; but from an examination of cast skins, in which the bands are more or less separated, the normal number appears to be 12, with the thirteenth segment represented by the unsclerotized caudal sucker.

The greatest morphological differences between species are found in the form and in the spine equipment of the pleural plates. In *Chalcura deprivata* (Fig. 99), those of the first two segments are rounded, whereas on the following six segments they terminate in long, posteriorly directed spines which are free, except at the base. The posterior margins of the plates are notched, and those of the fourth and fifth abdominal segments bear a second pair of spines. The paired spines of the latter segment are twice the length of those preceding. The sixth to ninth abdominal segments have the segmental bands but no pleural plates, and the caudal cerci are borne dorsolaterally on the eighth segment. Sensory spines and setae are as shown in the figure.

In *Schizaspidia manipurensis* (Fig. 99), the sensory spines of the pleural plates are much longer than in *Chalcura*, and *Kapala foveatella*, described by Ishii, has the distal portion of the plates of the fifth abdominal segment greatly produced and projecting beyond the end of the body. Several species of other genera show a less pronounced modification of the plates of this segment.

The spiracles, if present, are exceedingly small and difficult to distinguish. In *S. manipurensis*, the single pair is situated at the anterior margin of the prothorax.

The second-instar larva is known only in *S. tenuicornis*, *K. terminalis* and *Stilbula cynipiformis*. That of *Schizaspidia tenuicornis* (Fig. 100*B*) is shining white, with only nine distinguishable body segments, and the head is small, not heavily sclerotized, and situated ventrally. There are no sensory setae or integumentary spines. In *K. terminalis*, the body is bag-like, with only faint indications of segmentation, and a single pair of spiracles is situated at the anterior margin of the mesothorax. Parker's (1932) examination of the second exuviae of *Stilbula cynipiformis* revealed a lack of segmentation, several transverse rows of minute setae, and two pairs of spiracles.

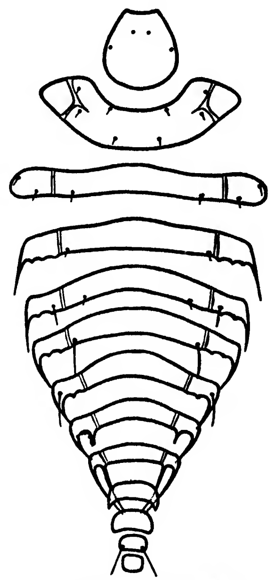


FIG. 98.—The first larval exuviae of *Chalcura deprivata* Wlk., showing the segmental plates, setae, and spines of the first instar. The bands are much more widely spaced than shown and the margins of the transparent intersegmental membranes are not indicated. (Original.)

The mature larvae, which are the third instar, are robust in all species, and they differ principally in the distinctness of segmentation, the presence or absence of dorsolateral tubercles, and the integumentary ornamentation. The larva of *Schizaspidia tenuicornis* shows no segmentation except for constrictions between the three principal parts of the body. This is true of several other species, but in *Eucharis* sp. the segmentation is distinct. Large dorsolateral tubercles on the first 10 body segments have been noted only in *Orasema*. All species bear an anal lobe, usually hemispherical in form, which may represent the last segment.

Although sensory setae and integumentary spines are lacking, yet the body is completely or partly covered with minute papillae or tubercles.

There are usually nine pairs of spiracles, situated on the second and third thoracic and the first seven abdominal segments, though in several species there are said to be only eight. The two pairs on the thorax are much the largest.

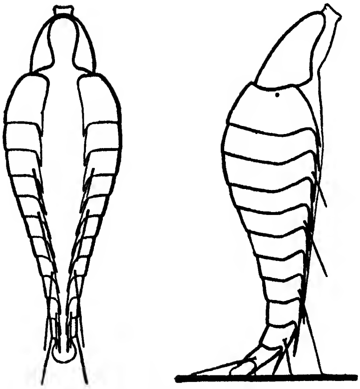


Fig. 99.—The first-instar larva of *Schizaspidia manipurensis* Claus., ventral and lateral views, the latter showing the larva in the erect waiting position. (*From Clausen*, 1928.)

It has been pointed out by Parker that the larva of *Stilbula cynipiformis* is devoid of tegumentary muscles, and this appears to be a normal condition in the family. In no species observed is the mature larva capable of ordered movement, and in many there is no visible physical reaction when they are disturbed.

The pupae of the Eucharidae present few distinguishing characters except in those species which have the scutellum produced into a bifurcate process, in which cases the pupal form is correspondingly modified (Fig. 100*D*). The abdomen of the female is very large and bears intersegmental ridges over the dorsum and sides. Some species of *Orasema*, *Schizaspidia*, *Kapala*, and *Chalcura* bear welts on the lateral portions of these ridges. These welts, or pustules, are most pronounced in *O. coloradensis;* the ridges of *O. viridis* are unmodified. The welts are globular in form and much constricted at the base and occur only on the posterior thoracic and petiolar regions, in *O. costaricensis*.

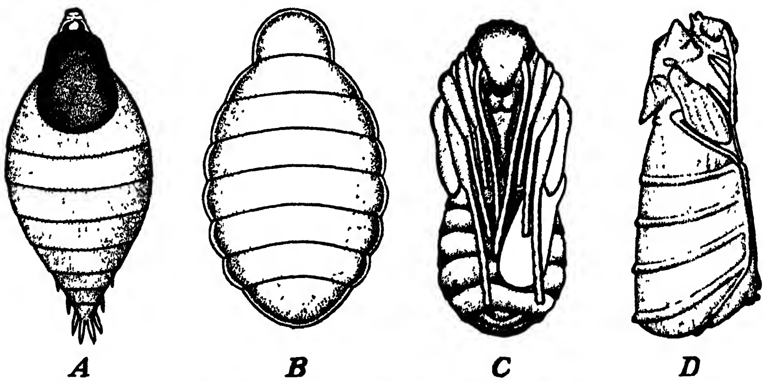


Fig. 100.—Immature stages of *Schizaspidia tenuicornis* Ashm. *A*, the first-instar larva; *B*, the second-instar larva; *C*, a *Camponotus* pupa bearing an early third-instar larva *in situ* beneath the wingpad; *D*, the pupa. (*From Clausen*, 1923.)

CHALCIDIDAE

The family Chalcididae is cosmopolitan in distribution and is represented most commonly by the genus *Brachymeria* (*Chalcis* of author's not Fabricius). Many of the species are of relatively large size and bear conspicuous markings. As primary parasites, they may be found attacking Lepidoptera, Diptera (Sacrophagidae and related families), and Coleoptera. The genus *Dirhinus* is a common prasite of fruit flies of the family Trypetidae in tropical regions. In the hyperparasitic role, many are found to attack Diptera (Tachinidae, etc.) and ichneumonoid Hymenoptera. Species of *Spilochalcis* are frequently reared from the cocoons of the latter

group. All the known species are solitary in habit and, with the exception of *Euchalcidia* and *Dirhinus*, develop internally. The different species of the family appear to have a very wide range of hosts. Thus, *B. intermedia* Nees attacks and will develop in almost any naked lepidopterous pupa, and *B. compsilurae* Cwf. and *B. fonscolombei* Duf. exhibit a similar catholicity of taste with respect to sarcophagid and other pupae.

From the point of view of natural control of insect pests, the benefits resulting from the reduction of blowflies and related forms and of Lepidoptera are fully offset by the losses from the hyperparasitic forms, and the family as a whole cannot be considered beneficial. Very few species have been utilized in biological control, and none has shown any marked degree of effectiveness.

BIOLOGY AND HABITS

Extended biological studies have been made upon a number of species, principally of the genus *Brachymeria*, some of which are primary parasites of Lepidoptera and others of Diptera, either in the primary or secondary role. The most informative accounts are on *B. femorata* Panz. (Faure, 1926; Kamal, 1938*a*), *B. intermedia* Nees (Dowden, 1935), *B. fonscolombei* Duf. (H. L. Parker, 1923; Roberts, 1933), *B. compsilurae* Cwf. (Dowden, 1935), and *Euchalcidia caryobori* Hanna (Hanna, 1934). These species cover, in general, the range of host preferences and relationships of the family.

Habits of the Adult.—The adults of species that develop in lepidopterous pupae emerge by biting away a hole at the anterior end, in a wing pad, or at the middle of the dorsum of the pupal shell, whereas those in puparia cut away the anterior end. Mating takes place very soon after emergence, and the gestation period is usually two to three days, though *B. fonscolombei* was found to be able to deposit eggs within three hours after emergence, and female progeny were secured from those deposited only eight to nine hours thereafter.

Adults of species attacking carrion-infesting hosts doubtless derive at least a part of their food from the meat juices. Feeding upon host fluids has been noted only in *B. intermedia* and *E. caryobori*, and in these instances it followed oviposition.

There is very little variation in the host stages attacked by species with similar preferences. Thus, the parasites of Lepidoptera oviposit in the young pupae, those attacking Diptera oviposit in the mature larvae, and *Euchalcidia* parasitizes either the mature larva or the pupa of its bruchid host. *B. compsilurae* oviposits in tachinid larvae while they are still within the dead bodies of their lepidopterous hosts, and *B. dalmani* Thoms. has the unusual habit, for this family, of attacking living locusts and ovipositing in the parasitic maggots contained in their bodies (Olsonfiev, 1929). *Spilochalcis pallens* Cress. oviposits directly

into the ichneumonoid cocoons. *Dirhinus giffardi* Silv. attacks the pupal stage of the fruit fly, rather than the mature larva.

The oviposition stimulus for the hyperparasitic and scavengerous species is usually not provided directly by the primary host. Females of *B. fonscolombei* are strongly attracted to maggots freshly dipped in meat juices, and oviposition is readily secured in droplets of these juices even in the absence of maggots. The females of *B. compsilurae* are particularly attracted to dead lepidopterous larvae or pupae containing tachinid maggots, but free individuals of the latter are avoided. They

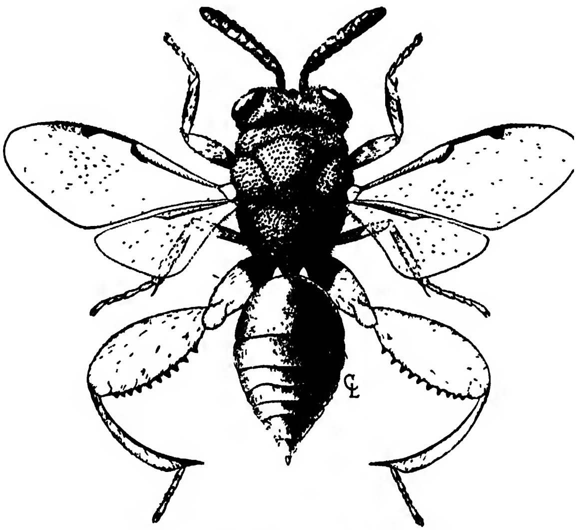


FIG. 101.—The adult female of *Brachymeria fonscolombei* Duf. (*From Roberts*, 1933.)

must be within a dead or dying host. The liquid excretions of the maggots themselves are particularly attractive to the females, and they will attempt to oviposit in droplets of this fluid.

The reproductive capacity of most species of the family is relatively low. Dowden states that the ovaries of *B. compsilurae* comprise only 12 ovarioles and that only a single egg attains maturity in each at one time. A maximum daily production of 12 eggs is thus indicated. *B. intermedia* has only 6 ovarioles, and its reproductive capacity is correspondingly less. Kamal indicates that about 180 eggs, deposited over a period of 60 to 70 days, is the maximum for *B. femorata*. *B. fonscolombei* has a much higher capacity; Roberts mentions finding 177 mature eggs in one female, though a maximum of only 80 progeny was secured. *Euchalcidia caryobori* is recorded as depositing up to 220 eggs, with an average of 102 for a series of females, at the rate of about 6 per day.

Adult life is relatively long in most species, with the exception of *B. fonscolombei*, which lives an average of only 11 days at summer temperatures. *B. compsilurae* and *E. caryobori* survive for about six weeks, whereas *B. femorata* and *B. intermedia* survive the winter and a considerable portion of the following season. Silvestri records keeping *D. giffardi* adults alive for at least five months.

Egg and Larval Development.—Incubation of the egg is complete in two or three days in all species that have been studied. Among the endoparasitic species, there is no appreciable increase in size during this period.

Superparasitization appears to be a frequent occurrence in the majority of species, as the females exercise no discrimination in the choice of hosts for oviposition. Usually, the surplus individuals are destroyed by combat during the first larval stage, though Roberts indicates that they may attain the second stage in *B. fonscolombei*. Two larvae of *Euchalcidia* may develop to maturity upon a single host provided that the eggs are placed upon opposite sides of the body. In competition, the older larvae are usually able to overcome the younger individuals.

The larval feeding period is very short, being completed in one week or less except in *B. compsilurae*, which has an active larval period of variable length, since development does not progress beyond the first instar until the host transforms to its pupal stage. Very shortly after this takes place, the feeding of the parasite larva results in the formation of a bubble-like area in the host body; and, after the first molt, it can usually be found in this space. In this and other species attacking dipterous hosts, the contents of the puparium are completely consumed, and the size of the adults is consequently variable and directly dependent upon that of the host individuals. In contrast to this is the habit of the species that develop in lepidopterous pupae. The contents of the latter are usually only partly consumed, for each one may contain sufficient food materials for several parasites. Only one parasite individual ever develops to maturity, and when feeding is completed the unconsumed portion is partitioned off from the cell in which pupation is to take place. This semifluid surplus is usually in the abdomen, for parasite feeding is limited to the anterior portion of the pupa, and in smaller host individuals it dries out quickly so that protection for the pupa is unnecessary.

Roberts has noted that *B. fonscolombei* emerges in the spring only from puparia that were formed the preceding autumn and that hosts that have passed the winter in the mature larval stage are unparasitized. This indicates an acceleration in development of the parasitized hosts, or rather a stimulus to pupation, comparable to that brought about by the braconid, *Alysia manducator* Panz., in *Lucilia* and other hosts.

The Life Cycle.—The cycle from egg to adult, in those species which have one complete generation or more during the summer, ranges from a minimum of 14 days in *Spilochalcis pallens* to 25 days in *B. compsilurae* under optimum conditions. In several species, the female requires 2 days longer than the male to complete its cycle.

Hibernation by *B. femorata* and *B. intermedia*, which parasitize Lepidoptera, is by the adult females only. In the latter species, a portion of the females of the early broods may also carry over the winter. The species of this genus that attack Diptera pass the winter as mature larvae in the puparia.

The number of generations that is produced each year depends quite largely on the habits and availability of hosts. *B. compsilurae* has only one generation in *Sturmia scutellata* R.D., whereas two or three develop in *Compsilura concinnata* L. *B. fonscolombei* is estimated to have approximately eight in blowfly larvae, of which host there is a supply available at all times during the season. *B. intermedia* may have two generations, and a partial third by utilizing several host species. *Spilochalcis pallens*, a hyperparasite of *Laphygma frugiperda* S. & A. through *Meteorus* and *Apanteles*, has several generations, for the primary parasites are available over a long period.

Sex Ratio and Parthenogenesis.—Incomplete data regarding several species of *Brachymeria* and *Euchalcidia caryobori* indicate that the sexes occur in approximately equal numbers. *B. compsilurae*, *B. intermedia*, *B. fonscolombei*, *S. pallens*, and *E. caryobori* produce only male progeny from virgin females.

Hanna (1935) has studied the effect of low temperatures upon the fertility of *E. caryobori* and finds that the exposure of pupae to subnormal temperatures results in a shrinkage of the ovarioles of the females, a marked reduction in egg production, and a high ratio of male progeny. The males are more quickly affected by adverse temperatures than the females, and the male progeny of females subjected to such conditions while in the pupal stage showed a high incidence of sterility.

IMMATURE STAGES

The eggs of the majority of species of the family are elongate and broadest at the anterior end, with both ends smoothly rounded, and the length is four to six times the maximum width. The micropylar area is represented by a small, slightly roughened area. In *B. fonscolombei* (Fig. 102*B*), there is a distinct slender peduncle, somewhat distended at the tip, at the anterior end. The egg of *B. compsilurae* (Fig. 102*A*) is distinguished by the possession of a membranous envelope which conforms to the shape of the egg body but is considerably larger, and the anterior end bears a roughened micropylar area similar to that of the egg proper (Dowden, 1935).

The first-instar larvae are of two types, the hymenopteriform and the caudate. The first-named is found in the ectoparasitic species and in those which are endoparasitic in lepidopterous pupae, and the caudate larva occurs among the species that

develop in dipterous pupae. The hymenopteriform larva of *B. intermedia*, which is characteristic of that type, is somewhat elongate, with a large, lightly sclerotized head and 13 distinct body segments of approximately equal length, each of which, except the last, bears three pairs of sensory setae and numerous cuticular spines, particularly on the venter. There are four pairs of spiracles, situated on the second thoracic and the first three abdominal segments. *B. femorata* and *E. caryobori* are said to have only two pairs of sensory setae on each segment.

The caudate first-instar larva, represented by *B. compsilurae* and *B. fonscolombei* (Fig. 102*C*, *D*) has 11 or 12 distinct body segments followed by a tail representing one-fifth to one-third of the total length. In *B. fonscolombei*, the tail apparently represents the fused twelfth and thirteenth segments. There appear to be no sensory

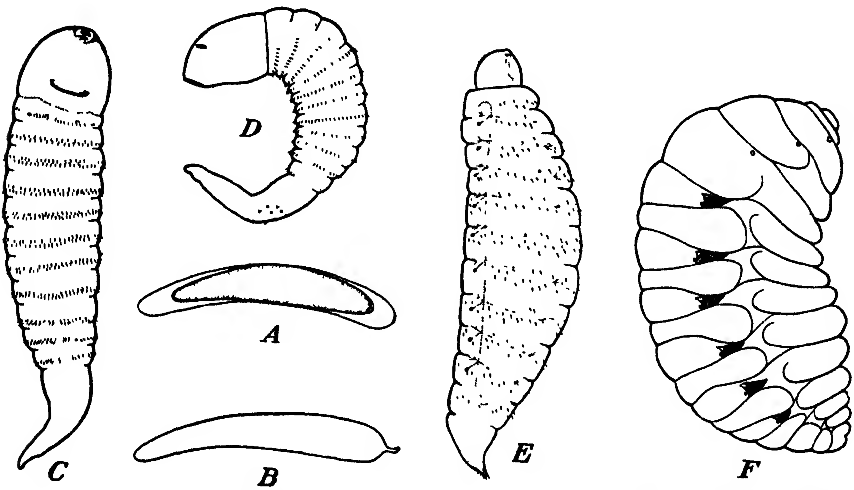


FIG. 102.—Immature stages of the Chalcididae. *A*, the egg of *Brachymeria compsilurae* Cwf. (*from Dowden*, 1935); *B*, the egg; *C* and *D*, the first-instar larva, ventral and lateral views; *E*, the second-instar larva; and *F*, the mature larva of *B. fonscolombei* Duf. (*from Parker*, 1924).

setae; but each segment bears a partial or complete ring of cuticular spines, and these occur also upon the tail, though irregularly distributed. An internal tracheal system is present, but there are no spiracles.

The second-instar larva is more robust, and, in the caudate form, the tail persists, though reduced in size. There appears to be no uniformity in spiracle number or arrangement. *B. compsilurae* still has none; *B. intermedia* retains the four pairs present in the first instar, of which those on the mesothorax are much the largest; and *B. fonscolombei* (Fig. 102*E*), *B. femorata*, and *E. caryobori* have nine pairs, situated on the second and third thoracic and the first seven abdominal segments.

The third-instar larvae show a further convergence of the two forms. In *B. compilurae*, the sensory setae first appear at this time. All species have the nine pairs of spiracles arranged as given above. The fourth-instar larva presents no distinctive features.

The fifth-instar larvae of *Brachymeria* and *Euchalcidia* are oval in outline, distinctly segmented, and yellowish-white in color. They bear no cuticular spines, but the sensory setae are present though minute. *B. fonscolombei* (Fig. 102*F*) and *B. compsilurae*, parasitic in dipterous puparia and having caudate first-instar larvae,

are further distinguished from others of the family by the possession, in the mature larva, of yellowish, wedge-shaped sclerotized plates situated just below the spiracles of the second to seventh abdominal segments. The function of these is unknown. The spiracles are as in the preceding two instars.

LEUCOSPIDAE

The family Leucospidae is closely related to the Chalcididae, and the adults are usually of large size, those of certain species being the largest known Chalcidoidea. The number of genera and species in the family is small; *Leucospis* is much the most common genus and is cosmopolitan in distribution. No species is at all abundant, and usually only occasional individuals can be found.

Relatively little is known regarding host preferences in the family. Several species of *Leucospis* have been reared from the cells of bees of the genera *Osmia*, *Megachile*, etc. They are solitary external parasites of the mature larvae. The first studies upon the habits of the family were those by Fabre (1886) in which the relationships between *L. gigas* F. and its host, *Megachile muraria* Retz., were determined.

BIOLOGY AND HABITS

The most complete account of the life history and habits of a member of the family is that by Graenicher (1906) of *L. affinis* Say, a solitary external parasite of the mature larvae of *O. pumila* Cress. in North America. Two generations are produced each year, and the winter is passed in the mature larval stage in the host cell. The adults emerge in the late spring and deposit their eggs during July. In preparation for oviposition, the female carefully examines with her antennae the surface of the twig or other object in which the bee cell is situated and then, having located it, lowers the tip of the ovipositor and drills through the wood and the cocoon wall. In several instances observed, the ovipositor penetrated 7 mm. of wood before reaching the cell of the host bee, and the time required for the operation was about ten minutes. The egg adheres to or is suspended by the tip of its stalk to the wall of the cell or to that of the host cocoon, if this has already been formed.

At hatching, the larva retains a hold upon the eggshell by means of the sucker-like tip of the abdomen and, by swaying about and extending the body in different directions, finally comes in contact with the body of the host larva, to which it attaches itself. Locomotion by this first-instar larva is in a looping manner, wherein the mouth and caudal sucker serve alternately for attachment. The long, segmental spines are considered to be more for protection against crushing in the cell than for aiding movement.

The first-instar larva changes its position frequently while feeding upon the host body, whereas the older individuals rarely move. The

entire body contents of the host larva are ultimately consumed. Pupation takes place within the host cell, and within the host cocoon if one has been spun. The parasite larva itself makes no cocoon.

The cycle from egg to adult, in the summer generation, is complete in approximately five weeks, the egg, larval, and pupal stages requiring approximately 3, 17, and 14 days, respectively. A portion of the mature larvae of the first generation may carry over until the following year. Normally, however, there appear to be two distinct generations each year.

Fabre has given an extended account of his observations upon the habits of the adult of *L. gigas*. The clay cells of *Megachile* are exceedingly hard, almost cement-like, and the female parasite often spends

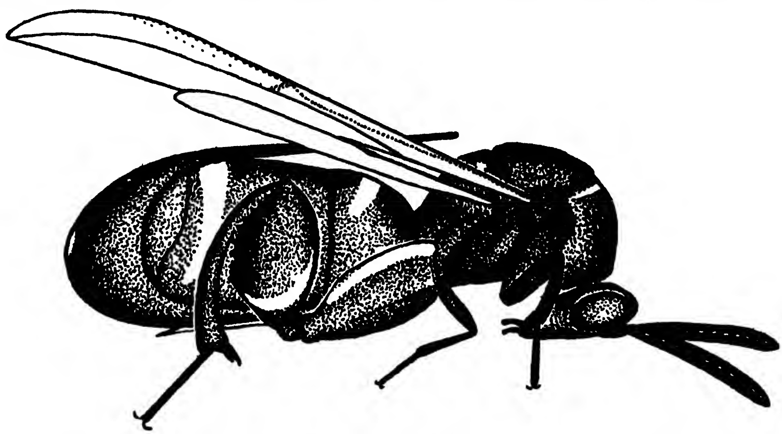


Fig. 103.—The adult female of *Leucospis japonica* Wlk. (Original.)

as much as three hours in drilling through it to the cell containing the larva. The instincts of the parasite are not infallible, however, and she will often penetrate a cell that is empty or that contains only a dead larva. She may even deposit an egg in one containing a dead larva, a habit noted by Graenicher in *L. affinis*, also. A number of eggs may be placed in one cell; but the young larvae are pronouncedly cannibalistic, and only one survives.

The female *Leucospis* carries the ovipositor and its sheaths in a groove extending along the median line of the abdomen, over the posterior end and terminating on the dorsum. In order to utilize the full length of the ovipositor which, in addition to the external portion, extends around the internal periphery of the abdomen, an ingenious arrangement is provided. The first and second abdominal segments became widely separated dorsally, and the arched ovipositor, thrusting against the thin intersegmental membrane, forces it outward in a decided bulge until the necessary portion is internal and the distal portion can

be brought into a perpendicular position. This adaptation at the moment of maximum distention is figured by Bischoff (1927). It is comparable to the provision found in *Rhyssa* and *Megarhyssa* of the Ichneumonidae for the same purpose, though in these the membranous sac appears between the sixth and seventh segments of the abdomen.

Berland (1934) states that *L. gigas* is apparently unisexual in France, whereas it is bisexual in North Africa. Other species in both regions have a normal sex ratio.

IMMATURE STAGES

The eggs have been described only for *L. gigas* (Fig. 104*A*) and *L. affinis*, and these are quite similar, being club-shaped and curved and bearing a dense covering of

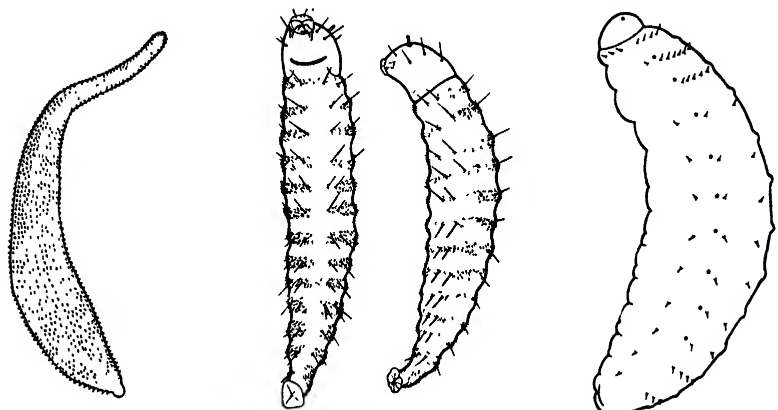


FIG. 104.—Immature stages of *Leucospis gigas* F. *A*, the egg; *B*, the first-instar larva, ventral and lateral views; *C*, the third-instar larva. (*From Parker*, 1924.)

minute papillae. The egg of *L. gigas* is exceedingly large, measuring 3.0 mm. in length. The anterior end is broadest, and the posterior portion is appreciably narrowed.

The first-instar larva of *L. gigas* (Fig. 104*B*), as described by Parker (1924), is elongate in form, with a large, moderately sclerotized head and 13 distinct body segments, of which the last is expanded into a retractile, sucker-like organ. The head bears prominent cylindrical antennae and four pairs of long sensory hairs. Each body segment bears three pairs of long and heavy spines and, in addition, a median band of minute setae. The four pairs of spiracles are situated on the second thoracic and first three abdominal segments.

The larva of *L. affinis*, as described by Graenicher, differs from the above in having only three pairs of sensory hairs on the head and two pairs on each body segment, and they are proportionately longer than in *L. gigas*.

The third-instar larva of *L. gigas* described by Parker (Fig. 104*C*) has a relatively small head bearing conical antennae, five pairs of sensory setae, and simple triangular mandibles. The segmental spines are as shown in the figure. The nine pairs of spiracles are situated at the anterior margins of the second and third thoracic and the first seven abdominal segments. The mature larva has not been described but probably differs from the third instar only in minor details.

SERPHOIDEA

The Serphoidea is perhaps the most consistent of the superfamilies of the Hymenoptera, both in host preferences and in relationships. They are all parasitic upon the immature stages of other insects. The most frequently encountered families are the Platygasteridae, parasitic internally in cecidomyiid larvae and homopterous nymphs, and the Scelionidae, exclusively parasitic in insect eggs. The hyperparasitic habit is found only in the Calliceratidae. The endophagous habit of development is general, with the exception of several genera of the latter family.

PLATYGASTERIDAE

There is an exceptional uniformity in adult form, habits, and host preferences and relationships among the species of this family. The

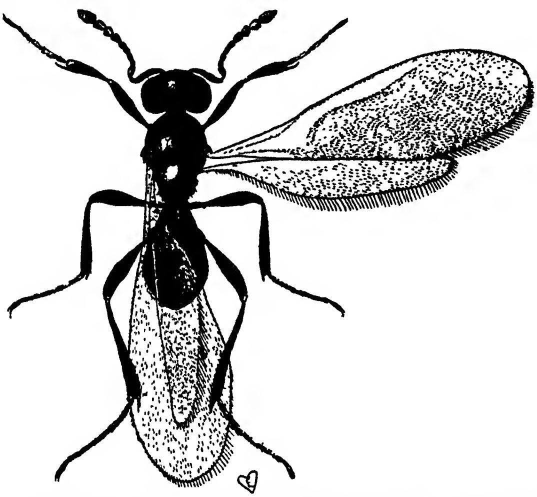


FIG. 105.—The adult female of *Platygaster zosine* Wlk. (*From Hill*, 1923.)

adults are of relatively small size and are usually black in color. The females of the genus *Inostemma* are conspicuous because of the curved, tubular "horn" which arises from the dorsum of the first abdominal segment and extends over the thorax to the head. The exceptionally long ovipositor lies in this horn when not extruded for oviposition. Biologically, the family has attracted a great deal of attention because of the occurrence of polyembryonic reproduction in the genus *Platygaster*.

Very few species have been utilized in the biological control of crop pests. The importation of *Misocyclops marchali* Kieff. into New Zealand from Europe in 1925 is reported to have resulted in an appreciable reduction in infestations of the pear midge, *Perrisia pyri* Bouché.

HOST PREFERENCES

The great majority of species that have been associated with their hosts are parasitic in the larvae of Cecidomyiidae. Members of the genus *Amitus* are known to parasitize Aleyrodidae, and those of *Allotropa* are perhaps the dominant parasites of *Pseudococcus* in the Far East. Occasional species have been recorded from Lepidoptera, Hymenoptera, and Coleoptera, but these records require further verification.

BIOLOGY AND HABITS

The more extensive contributions to the biology of the Platygasteridae have been the following:

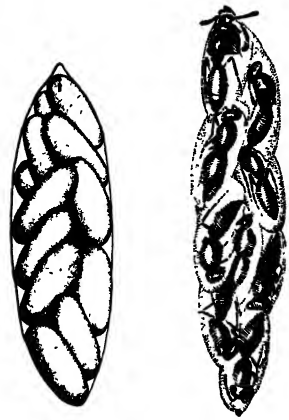
Inostemma boscii Jur.	Myers (1927)
Inostemma piricola Kieff.	Marchal (1906)
Leptacis rhanis Wlk.	Marchal (1906)
Platygaster spp.	Ganin (1869), Kulagin (1898)
Platygaster dryomiae Silv.	Silvestri (1921)
Platygaster herrickii Pack.	Hill & Emery (1937)
Platygaster hiemalis Forbes	Leiby & Hill (1923), Hill (1926)
Platygaster lineatus Kieff.	Marchal (1906)
Platygaster ornatus Kieff.	Marchal (1906)
Platygaster zosine Wlk. (*minutus* Lind., *vernalis* Myers)	Marchal (1897, 1903, '04), Hill (1923), Leiby & Hill (1924)
Trichacis remulus Wlk.	Marchal (1897, 1906)

All species are parasitic internally and are usually either consistently solitary or gregarious, very few being solitary in some host individuals and gregarious in others. The hosts are invariably attacked in a very early stage, and death generally occurs in the pupal stage, though a few species of the family bring this about before pupation.

Oviposition.—In attack upon cecidomyiid hosts the majority of parasites of this family deposit their eggs within the host egg, though a few, such as *P. dryomiae* and *Trichacis remulus*, may at times oviposit in the newly hatched larvae and *Leptacis rhanis* consistently does so. Oviposition in the host egg, with development and emergence taking place in later stages, was first definitely established by Herrick (1841) for *P. hiemalis*. Many years previously, however, Kirby (1800) had presented evidence that this must be the habit of *Isostasius inserens* Kirby, a parasite of *Phytophaga*, though he did not actually observe oviposition. Herrick's observations were repeated and confirmed by several workers dealing with *P. hiemalis* and *P. zosine*, but this manner of oviposition and development was not given credence until the publication of Marchal's exhaustive studies from 1896 to 1906 on the biology of *Ageniaspis* and several species of Platygasteridae.

Amitus hesperidum variipes Silv., a gregarious parasite of the aleyrodid, *Aleurocanthus spiniferus* Q., in tropical Asia, oviposits in the young larvae immediately after hatching and largely before they become fixed to the leaf (Clausen, 1934).

When ovipositing in exposed host eggs, the female usually stands over the egg, and parallel with it and inserts the ovipositor by a backward thrust. Concealed eggs or larvae are reached by probing with the long, extensible ovipositor. The females of some solitary species appear able to exercise a considerable degree of discrimination and seldom deposit more than a single egg in one host. Experiments by Hill with *P. hiemalis* indicated that the female was able to recognize eggs which she had previously attacked and refrained from placing a second egg in them but that she was unable to recognize those attacked by another female. A similar reaction was noted in *P. zosine.* The majority of species are solitary in habit and consequently deposit only a single egg at each insertion of the ovipositor, though *P. hiemalis* and *P. variabilis* Fouts normally deposit four to eight.



A B

FIG. 106.—*A*, cocoons of *Platygaster hiemalis* Forbes within a hessian fly puparium, the latter indicated by outline only (*from Hill,* 1926); *B*, adults of *Platygaster* in a host puparium just prior to emergence (*from Bureau of Entomology and Plant Quarantine*).

In egg-ovipositing species the location of the parasite egg in the host embryo is variable, though fairly constant for any given species. The eggs of *Inostemma boscii* and *I. piricola* are found in the brain, whereas that of *Trichacis remulus* is in the posterior portion of the nerve chain. Adler (1908), however, states that the egg of *I. boscii* is found in the peduncle of the host egg, and some are even deposited externally. Eggs deposited in the fluids between the chorion and the embryo cannot develop to maturity. *P. zosine* oviposits in the mid-intestine of the host and cannot develop elsewhere, whereas a number of species, such as *Misocyclops marchali* Kieff. (Dumbleton, 1934), *P. lineatus*, and *P. ornatus*, place the egg in the general body cavity. The exact placement of the egg in a particular portion of the embryonic mass requires an exceptional degree of accuracy on the part of the female at the time of oviposition. It is accomplished in part by orientation of the body to conform to the long axis of the egg, which greatly facilitates the location of the nerve chain or the intestine. The length of the ovipositor may also play a part, and it is probable that tactile organs at the tip of the ovipositor also are of some aid. Freshly laid host eggs are not suitable

for oviposition, for the lack of embryonic development precludes the possibility of the parasite egg being associated with a particular organ or cavity of the body.

Monembryonic and Polyembryonic Development.—*P. herrickii* Pack., a parasite of the hessian fly in North America, may be considered as representative of the Platygasteridae that undergo monembryonic reproduction (Hill and Emery, 1937). It is normally solitary, though occasionally two or three individuals may develop in the same host. Embryological development takes place concurrently with that of the host. The egg lies free in the body cavity, and at no time is the embryo surrounded by a cyst of host tissue. A number of "pseudogerms" are

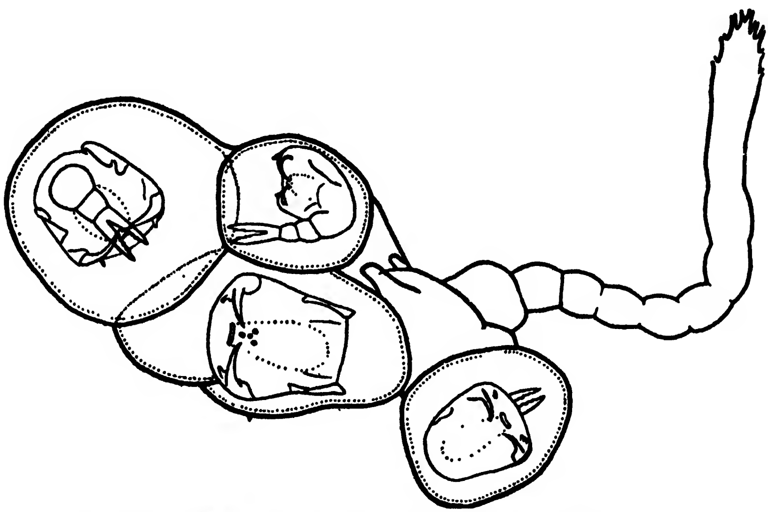


Fig. 107.—The nervous system of a larva of *Contarinia pirivora*, showing four brain cysts containing first-instar larvae of *Inostemma piricola* Kieff. (*Redrawn, after Marchal, 1906.*)

developed from the paranuclear bodies, and these develop superficially in the same way as true germs. They attain considerable size and at the time of hatching are released into the body cavity of the host, where they undergo further growth, attaining an average diameter of 0.14 mm. Disintegration finally takes place, and they are consumed by the developing parasite larva. The number of these pseudogerms in hosts containing a single first-instar larva averages about twenty-five.

The eggs that are placed in the brain or the nerve chain become enveloped by a cyst of host tissue (Fig. 107), often involving striking proliferations, which surrounds the developing embryo or embryos until the first larval stage is reached and they emerge into the host body for direct feeding. These cysts may be compared to certain animal galls produced as a result of the presence of various parasitic organisms. In the case of

the majority of species that place the egg in the general body cavity, it becomes attached to some organ, such as a salivary gland or fat body, and a similar cyst is formed about the developing embryo. *P. zosine*, however, lies in the intestine of the host and is free-floating at all times until the intestinal wall is broken and gross feeding begins.

Polyembryonic reproduction in the family is limited, so far as known at present, to a series of species of the genus *Platygaster*, all of which develop in Cecidomyiidae. In the genera *Amitus* and *Allotropa*, attacking Aleyrodidae and *Pseudococcus*, respectively, the general habits and the number of individuals developing in each host point to the possibility of this mode of reproduction. A number of species that are solitary show this mode of development in their early stages, thus paralleling the development of *Macrocentrus ancylivorus* Roh., of the Braconidae.

The host species are all of relatively small size, and consequently the enormous numbers of progeny produced in a single host by several Encyrtidae are not found in this family. The maximum recorded is an average of 18 in the case of *Platygaster felti* Fouts in *Rhopalomyia sabinae* Felt, but producing only 11 in *Walshomyia texana* Felt. *P. variabilis* in *Rhopalomyia* produces an average of 15, and *P. zosine* and *P. hiemalis*, parasites of the hessian fly, average 7.9 and 6, respectively.

The simplest form of polyembryony is found in *P. hiemalis*, and it results in the production of not more than two individuals from each egg. The female parasite deposits a group of five to eight eggs in each host egg and from these an average total of 6.3 individuals attain maturity. About one-third of these eggs fail to develop beyond the cleavage nucleus stage, presumably because they have not become invested by host tissue and consequently do not receive the food materials essential to their further development. An additional portion of the eggs develops monembryonically in a highly specialized manner comparable, in most respects, to the normal course of development of *L. rhanis*, *T. remulus*, and *P. ornatus*, previously investigated by Marchal. According to Leiby, *P. variabilis* undergoes twinning in the same way as does *P. hiemalis*. The occurrence of both forms of embryonic development in the same species is unknown elsewhere in the order and is believed by Hill to furnish a clue to the origin of polyembryony.

Though aborted eggs occur only in *P. hiemalis*, yet, in other species that produce a larger number of individuals from each egg, aborted germs, blastulae, and larvae may be found. The number of these in any species of *Platygaster* is very small in comparison with the Encyrtidae of polyembryonic habit.

In the early stages of development, as has been mentioned, the trophamnion envelops the embryonic portion of the egg and later serves as a sheath through which the food elements essential to the development

of the embryos to the larval stage are derived from the blood of the host. The growth of the trophamnion during embryonic development permits the germs to divide, and these later become invested individually by portions of it. The above manner of obtaining nourishment is not peculiar to the Platygasteridae but is found in many other parasite groups in which development is monembryonic. Such feeding is necessary where no yolk material is provided in the egg itself. The amount of food material taken from the host body is relatively small, and consequently the host is not appreciably affected by the presence of the young parasite bodies. The physical changes preparatory to pupation of the host provide the stimulus for the completion of embryonic development and for the attainment of the direct-feeding larval stages.

The subject of mixed broods and their origin in the polyembryonic Platygasteridae has attracted the attention of a number of investigators; some difference of opinion prevails as to the manner in which they arise, particularly where the proportion of males is small. In *P. hiemalis*, 80 per cent are mixed broods and 20 per cent pure female broods. In 71 per cent of the rearings, the females exceeded the males in number. In *P. zosine*, the great majority of broods are of a single sex. *P. felti* (Patterson, 1919, '21*b*), on the contrary, showed 90.5 per cent of the broods to be mixed, more than half of these contained only a single male, and no pure male broods were found. In not a single instance did the males outnumber the females in a mixed brood. In *P. variabilis*, 92 per cent of the broods proved to be mixed, and only a single pure male brood was found in a total of 217. Marchal, Leiby, and Hill are of the opinion that males in mixed broods develop as a result of duplicate oviposition, in which at least one of the eggs has not been fertilized. Patterson, however, is of the opinion that they arise as a result of abnormal behavior of the two sex chromosomes during the early cleavage divisions of the egg.

Larval Development.—The free-living first-instar larva feeds directly upon the body fluids, and in a few species it has been shown to ingest tissues as well. The first-instar larvae of the cyclops form is capable of considerable movement, which is accomplished by ventral or backward thrusts of the caudal processes and the posterior portion of the abdomen. No evidence has been presented that the large falcate mandibles are utilized for feeding; they may be for fighting purposes instead, as has been established in the case of other groups possessing similar mandibles. The embryonic stages require a relatively long period of time for development, whereas the stage from emergence of the first-instar larva from the trophamnion to the death of the host is usually relatively short. In the gregarious forms, the mature larvae form individual cells in the

host body; these are distinctly evident externally. Each larva lines its cell with silk, forming a delicate cocoon.

The degree of inflation of the host body is not comparable with that produced by the polyembryonic Encyrtidae. The hosts that are killed as mature larvae become appreciably darkened in color, so that they have a considerable resemblance to puparia. In some species, the parasitized puparia are smaller than normal and distinctly irregular in form, indicating that the parasite larvae were sufficiently advanced appreciably to interfere with the normal processes of pupation. Kulagin (1892), in discussing a species under the name of *P. instricator* but which has apparently not been described, at least not under that name, states that the cecidomyiid host pupates normally if it contains only a single parasite, whereas it dies without pupating if several are present. It is possible that two species were represented in the material under observation, which would account for this difference; this is indicated also by the presence of two egg forms, one in the fatty tissue and the other in the digestive tract.

Life Cycle.—The majority of species of Platygasteridae that have been studied have only a single generation each year, in spite of the fact that the host may have several generations during that period. This is illustrated by the species of *Platygaster* attacking the hessian fly in North America. The single brood of adults of *P. herrickii* and of *P. zosine* normally emerge early in the spring, whereas that of *P. hiemalis* emerges in the autumn. The host, however, has several generations each year. This requires the parasites to pass a considerable portion of the year in a more or less inactive condition. *P. herrickii* oviposits in the spring and requires practically the entire season for larval development, the adult stage being attained late in the autumn. *P. zosine*, with an annual cycle, also, reaches the mature larval stage in June, and there is an extended period within the cocoon before the adult stage appears. In the case of *P. hiemalis*, the eggs are deposited in the autumn, and the embryos persist within the host larvae until the following season and do not attain the free larval stage until June or July, after which pupation takes place in August. *Inostemma boscii*, on the other hand, has two generations annually, corresponding to the cycle of the host, and *Leptacis rhanis* has a partial second, the main brood of adults emerging in May.

P. dryomiae, *P. ornatus* Kieff. and *P. hiemalis* pass the winter in the embryonic stage within the body of the living host. *L. rhanis* and *I. boscii* hibernate as mature larvae in the cocoons, whereas *P. lineatus*, *P. herrickii*, *P. zosine*, and *I. piricola* transform to the adult stage during the autumn but do not emerge from the host puparium until the following spring.

Reproductive Capacity and Sex Ratio.—The reproductive capacity of some Platygasteridae is exceptionally high, even without the multiplication brought about by polyembryonic reproduction. Gravid females of *P. hiemalis* were found by Hill to contain an average of 3,322 eggs in the ovaries which, on the basis of 1.5 individuals developing from each egg, results in 4,983 progeny for each female. *P. zosine*, on the other hand, contained only 228 eggs, each of which may produce 8 individuals, or a total of 1,224. *P. hiemalis* was observed by Hill to oviposit 160 times in one day, which on the basis of 4.2 eggs per insertion would give a total of about 675 eggs during that period, resulting finally in more than 1,000 progeny.

The sex ratios of the species in which they have been determined usually reveal a preponderance of females. In *P. zosine* and *P. herrickii*, the sexes are represented by approximately equal numbers, whereas the females predominate in *P. hiemalis* by 2 to 1 and in *P. felti* and *P. variabilis* by 6 to 1. In all species that reproduce monembryonically, parthenogenetic reproduction results in male progeny only.

IMMATURE STAGES

The platygasterid egg is always of minute size, ranging in length from 0.02 to 0.1 mm. The main body is usually lemon-shaped, with a stalk at the anterior end which, in *L. rhanis* (Fig. 108*A*), is three times the length of the egg body. In other species, this stalk is shorter, and the extreme is shown in *P. herrickii* (Fig. 108*C*) which has the posterior end somewhat attenuated and bears several short flagellum-like processes at the anterior end. Several species that have a pronounced stalk also bear a blunt protuberance at the posterior end.

The first-instar larvae of the polyembryonic species is the form that frees itself from the enveloping trophamnion; it does not necessarily differ from those of the monembryonic sphecies. There are two types of larva of this instar, the first being hymenopteriform and the second cyclopoid. The hymenopteriform first-instar larva is elongate-oval to almost spherical in form and distinctly segmented, with the head small, the mandibles relatively large, no fleshy processes on the body, and three pairs of spiracles, situated on the second and third thoracic and the second abdominal segments. *P. hiemalis* (Fig. 109*B*) *P. ornatus*, and *P. dryomiae* are of this type. A large discoidal body replaces the spiracle on the first abdominal segment, and a spiracular branch leads to it. In *P. zosine* (Fig. 109*A*), the body is more elongate, with a constriction between the head and thorax, but it lacks any further indication of segmentation. There are no spiracles.

The cyclopoid type of first-instar larva is characterized by a cephalothorax usually larger than the remainder of the body and somewhat flattened dorsoventrally, which bears enormous falcate mandibles and conspicuous antennae. The abdominal segments are narrowed and reduced in number. The mandibles are widely spaced, being set near the lateral margins, and they lie transversely. The body terminates in one or more fleshy processes of diverse form. This type was first studied and figured by Ganin (1869) (Fig. 110) for several species parasitic in cecidomyiid larvae; it was described as "cyclops-like." Two of them described by him have a pair of large fleshy processes lateroventrally on the cephalothorax near the posterior margin, and the caudal segment bears two or more long spine-like processes which themselves are

armed with numerous spines. A similar larva has been described by Marchal for *Leptacis rhanis* (Fig. 108*B*). A second form described by Ganin shows the caudal appendage bifurcate, with the inner margins serrate. That described by Marchal for *Inostemma piricola* (Fig. 109*C*) bears a close resemblance to it. In *P. lineatus*,

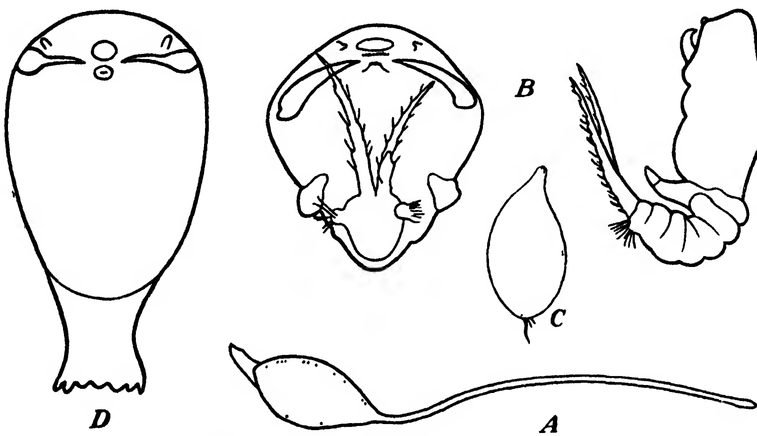


FIG. 108.—Immature stages of the Platygasteridae. *A*, the egg of *Leptacis rhanis* Wlk.; *B*, first-instar larva of same, ventral and lateral views (*after Marchal*, 1906); *C*, egg of *Platygaster herrickii* Pack. (*from Hill and Emery*, 1937); *D*, first-instar larva of *Misocyclops marchali* Kieff. (*after Marchal*, 1906).

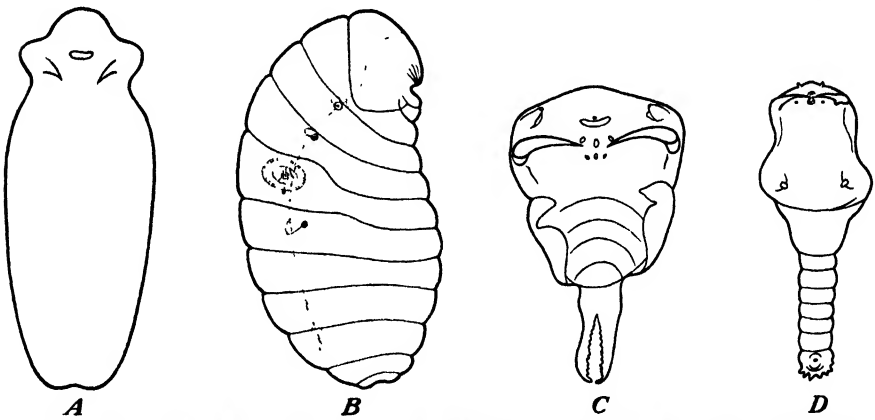


FIG. 109.—First-instar larvae of Platygasteridae. *A*, *Platygaster zosine* Wlk. (*from Hill*, 1923); *B*, *P. hiemalis* Forbes (*from Hill*, 1926); *C*, *Inostemma piricola* Kieff.; *D*, *Platygaster* sp. (*after Marchal*, 1906).

P. herrickii, *Misocyclops marchali* (Fig. 108*D*), and *Sactogaster pisi* Foerst. (Kutter, 1934), the caudal appendage is broad, terminating in a pair of lobes which, in the last-named species, bear short, heavy spines. In *T. remulus* (Fig. 111), the abdominal segments are very narrow and the caudal process is short and bilobed, with the tips rounded and curved inwards. An undetermined species of *Platygaster* figured by Marchal (Fig. 109*D*) has the last abdominal segment somewhat expanded, with the posterior margin serrate. In some species, such as *M. marchali*, the paired fleshy processes that generally occur ventrally on the cephalothorax are entirely lacking.

Spiracles are not known to occur upon any cyclopoid larvae, in contrast to the three pairs occurring upon most hymenopteriform larvae of the family.

There is considerable question as to the body parts that make up the so-called cephalothorax of the cyclopoid larva. Some authors consider it to consist only of the head, and illustrations show the mandibular muscles attached near the posterior base, though Marchal considers it to include the thoracic segments, also. The fleshy paired ventral processes are presumably borne on the first thoracic segment. The fact that

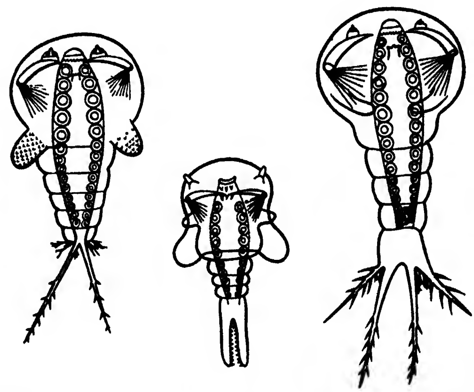


FIG. 110.—First-instar larvae of several species of Platygasteridae from cecidomyiid larvae. (*Redrawn, after Ganin*, 1869.)

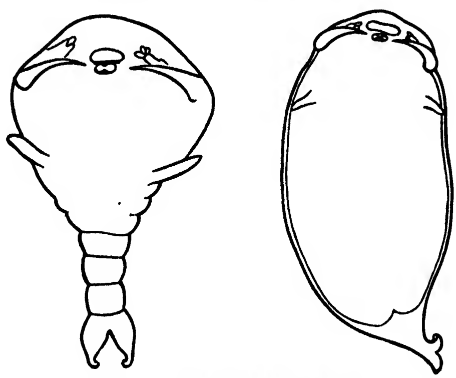


FIG. 111.—First-instar larvae of *Trichacis remulus* Wlk., that at right much distended after extensive feeding. (*Redrawn, after Marchal*, 1906.)

the visible segments following the cephalothorax number only five to seven lends weight to this conclusion and accords with the reduced number of body segments found in the mature larva.

The consideration of the instars following the first is complicated by a variation in the number of molts recognized among the different species. According to Hill, *P. hiemalis* has only a single larval instar. It is of considerable size when separation is effected from the trophamnion, and a relatively slight growth brings it to larval maturity. In *P. zosine*, according to the same author, there is only one molt, and the mature form immediately succeeds the first instar.

The second instar, as here discussed, includes only those of species in which three larval instars have been noted. That described and figured by Ganin for *Platygaster*

sp. is oval in form with no indication of segmentation; during its early period, it is enclosed within the distended skin of the preceding instar. There are no fleshy or cuticular processes of any sort, and no open spiracles are present. Other species that have been studied by various authors possess second-instar larvae that likewise present no distinguishing characters. The mandibles are small in all species.

The mature larvae, which may be of the first, second, or third instar, depending on the species under consideration, present no characters by which they may be readily separated. The body is oval in form and distinctly segmented and comprises the head and 10 or 11 body segments. No cuticular spines or fleshy processes are to be found. The mandibles are small and widely spaced. The tracheal system possesses three pairs of spiracles, situated on the second and third thoracic and the second abdominal segments. The first abdominal segment bears the large discoidal body mentioned in the discussion of the first-instar larva of *P. hiemalis* and others. This organ has been detected only in species of *Platygaster* but may occur in other genera also.

SCELIONIDAE

The family Scelionidae comprises a considerable number of species; practically all these are of small size and reveal an exceptional uniformity in host preferences and habits and in the morphological characters of the immature stages. All the known species are parasitic in the eggs of other insects, particularly of Lepidoptera, Hemiptera, Orthoptera, Diptera (Tabanidae), and of the Arachnida. Occasional species attack the eggs of Coleoptera and Neuroptera (Chrysopidae). The majority are solitary in habit. The more common genera are *Phanurus*, parasitic in the eggs of several orders, *Telenomus*, mainly in those of Lepidoptera and Hemiptera, *Scelio* in orthopterous eggs, and *Rielia* in mantid eggs. Several species of *Microphanurus* have been reported as reared from the eggs of Coccidae. Species of the genera *Tiphodytes* and *Limnodytes* are aquatic in habit and develop in the eggs of the water boatman (*Gerris* spp.).

Representatives of the family have been successfully utilized in several instances for the control of crop pests. *Aphanomerus pusillus* Perk., introduced into Hawaii from Australia in 1904 as a parasite of the torpedo bug, *Siphanta acuta* Wlk., was responsible for the complete control of that pest. Another importation into Hawaii, *Scelio pembertoni* Timb. from Malaya from 1930 to 1931, is credited with effecting a decided reduction in the population of *Oxya chinensis* Thunb. More recently, the importation of *Microphanurus basalis* Woll. into New South Wales from Egypt in 1934 has resulted in a high parasitization and gives evidence of appreciable field control.

In several cases, it has been found possible to increase the effectiveness of native species. Parman (1928) undertook the liberation of *Phanurus emersoni* Gir. in sections of Texas where it previously did not occur, and a marked reduction in the population of the horsefly, *Tabanus hyalinipennis* Hine, was attained. Okada and his associates (1934)

in Japan report a considerable increase in parasitization of eggs of the rice borer, *Chilo simplex* Butl., through early colonization of *P. beneficiens* Zehnt.

BIOLOGY AND HABITS

The more detailed accounts of the biology and habits of species of the family are of *Eumicrosoma benefica* Gahan (McCulloch and Yuasa, 1914, '15), *Rielia manticida* Kieff. (Chopard, 1920, '23), *Telenomus cosmopeplae* Gahan (Balduf, 1926*c*), *T. fariai* Costa Lima (Costa Lima, 1928), *T. ulyetti* Nixon (Jones, 1937), *Scelio pembertoni* Timb. (Pemberton, 1933), *S. fulgidus* Cwf. (Noble, 1935, '38*c*), and *Microphanurus basalis* Woll. (Noble, 1937; Kamal, 1938*b*).

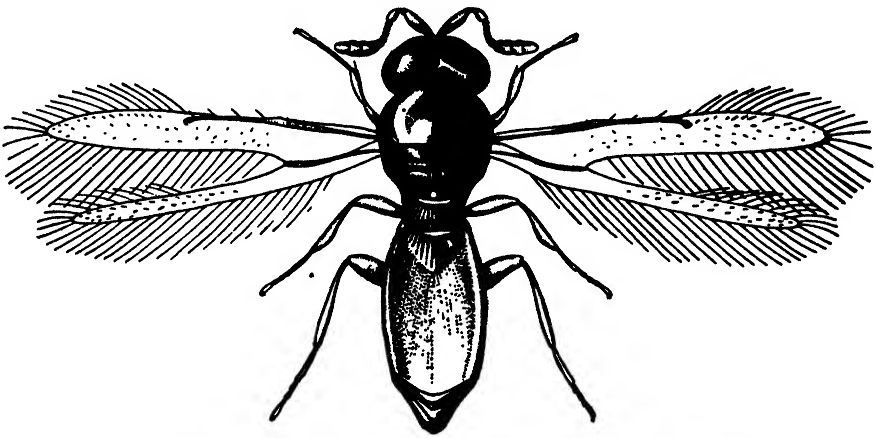


FIG. 112.—The adult female of *Eumicrosoma benefica* Gahan. (*From Gahan*, 1913.)

Oviposition.—Many species of the family appear to exercise a considerable degree of selectivity in oviposition. Morrill (1907) states that the female of *T. ashmeadi* Morrill, after the completion of oviposition, scrapes the surface of the host egg with the ovipositor, making a number of circular lines about the point of penetration. This is said to be probably to "mark the parasitized egg so that it can be detected as unsuitable for further attack by its own species." Costa Lima mentions the same behavior by the females of *T. fariai*. Voukassovitch (1925*a*) discusses this point in relation to *Trissolcus simoni* Mayr, which develops in the eggs of *Eurydema*, and states that the females will examine carefully all eggs which are encountered and will not attack those previously parasitized. Even where this has been very recent, it is quickly detected by the insertion of the ovipositor. The opinion is expressed that the marking of the eggs with the ovipositor serves to prevent later attack by other females. In contrast to the pronounced selectivity shown by *Telenomus*, there appears to be a decided lack of discrimination in

Eumicrosoma benefica, for the females have been observed to attempt oviposition in host eggs containing various stages of their own species, resulting in frequent superparasitization, and they even insert the ovipositor in empty eggshells, etc. Several females of *Microphanurus basalis* have been observed ovipositing simultaneously in a *Nezara viridula* egg, and frequently several eggs or first-instar larvae are found in one host egg.

A number of instances of phoresy have been recorded in the family wherein the adult female of the parasite attaches herself to the female of the host species and clings tightly to her until oviposition takes place, whereupon the parasite leaves the body and immediately attacks the eggs. This habit is discussed at length by Rabaud (1922) and Chopard, as observed in *Rielia manticida*, which develops in the eggs of Mantidae. The winged females of *Rielia* attach themselves by the mandibles near the base of the wings or at the extremity of the abdomen of the adult mantids, and after this is effected the wings are discarded. The parasites may be found upon both male and female mantids but are most common upon the latter. Oviposition by the host takes place during the autumn months; at the time the egg mass is being formed and before the frothy covering has hardened, the female parasite descends into it and deposits her eggs singly in those of the host. After oviposition is completed, she attempts to regain her position on the mantid body. The parasites attach themselves to the mantids very shortly after their own emergence and consequently may remain inactive in that position for several months before host oviposition takes place. These adult females are stated to be true parasites of the mantid adults inasmuch as they feed upon the body fluids during the waiting period.

Brues (1917) records a similar habit in *Lepidoscelio viatrix* Brues, which develops in the egg pods of locusts of the genus *Colemania* in India. The females were found attached by the mandibles to the intersegmental membranes between the abdominal plates. Noble mentions that several field-collected females of the plague grasshopper had females of *Scelio fulgidus* clinging to the abdomen.

Van Vuuren (1935) has recently given an extended account of phoresy in *Phanurus beneficiens*, a solitary parasite of the eggs of the rice borer, *Schoenobius bipunctifer* Wlk., and other rice borers, also, in the Far East. Trap collections of adult moths at dusk revealed that 15 per cent bore *Phanurus* females upon their bodies. About one-third of these wasps were found upon the wings. The scales were rubbed off at the point of attachment, forming a distinct 8-shaped mark. No parasites could be found upon male moths. The host eggs are attacked immediately after deposition. It would appear that the above relationship, though apparently common in Java, is not obligatory, for various other investiga-

tors have conducted extensive life-history studies upon this species and have secured direct oviposition readily.

The majority of species of the family show a decided preference for freshly laid host eggs in which to oviposit, a habit that is common to the Trichogrammatidae, also, though not to so pronounced an extent. In *R. manticida* and *P. beneficiens*, as already mentioned, oviposition takes place only immediately after egg deposition by the host female. Jones has recently found that the females of *T. ulyetti* Nixon show a preference for *Heliothis* eggs from a few hours to 1 day old but will, under necessity, oviposit in those up to 2 days old. The latter figure represents nearly half the incubation period of the host egg, which is 5 to 5½ days.

Eumicrosoma benefica, which attacks the eggs of the chinchbug, *Blissus leucopterus* Say, in North America, prefers eggs that are one to three days old, and successful parasitization becomes less frequent in those which are older. Hatching occurs in less than one day, often in a few hours, and larval feeding is complete in three days. *P. emersoni* refuses to oviposit in *Tabanus* and *Chrysops* eggs that are more than six hours old.

There are a number of exceptions to the above rule regarding the stage of development of the host eggs at the time of attack. According to Costa Lima, *T. farai* is able to develop successfully in eggs of *Triatoma* even though the embryos are well-advanced at the time of attack. *Scelio pembertoni* oviposits in *Oxya* eggs in all stages of development.

Oviposition by *Scelio* in orthopterous eggs deposited in masses in the soil presents several points of interest. The female of *S. pembertoni* penetrates the loose soil above the egg mass; she may then bite out a hole in the egg pod, after which she turns about and inserts the ovipositor. This organ may be extruded to a length twice that of the body, and consequently all eggs in the mass are within reach. From three to five hours may be spent upon one egg mass without withdrawing the ovipositor. The females of *S. fulgidus* are present in the field at the time the grasshoppers are ovipositing, and they may even make their way down to the egg mass before it is completed. After the grasshopper female has departed, the parasite bites out a tunnel through the secretions covering the mass and along the side, stopping periodically to oviposit. Although the host eggs are available for a large portion of the year, yet the greatest parasite activity takes place during the 24 hours immediately following host oviposition.

Larval Development.—The more exact information regarding the development of the early stages is that for *Telenomus ulyetti* in *Heliothis* eggs. The parasite egg is found floating free in the yolk between the amnion and the serosa, and the young larva lies in the outer yolk layer and is attached by its mouth parts to the serosa. Development of the

host embryo is not affected by the first-instar parasite larva, for it is not dependent upon that part of the yolk material upon which the latter feeds. The second-instar larva attacks the body of the embryo, and eventually the entire egg contents are consumed. It is thus seen that the parasite larva, to complete its development successfully, must attain the second instar before the body wall of the embryo has hardened sufficiently to become invulnerable to the parasite's mandibles. If this hardening has taken place, the parasite larva dies from starvation, the host embryo completes its development, and normal hatching takes place. It is of particular interest that this parasite is unable to develop in infertile host eggs. *Microphanurus basalis*, on the contrary, develops quite as readily in dead *Nezara* eggs showing no embryological development at the time of death as in live eggs in an advanced stage of development. This would seem to indicate either that development of the early-stage larva normally takes place within the embryo or that the larva itself is capable of penetrating it at any stage of development.

The change in coloration of the parasitized host egg is distinct and contrasts strongly with the changes undergone by healthy eggs. Within five to six days after parasitization, the eggs of most species become gray or grayish-brown, or, in only a few instances, black. Eggs parasitized by Scelionidae can usually be distinguished from those containing Trichogrammatidae by this means, the latter quite generally becoming black.

In spite of the sac-like form of the first-instar larva it is capable of considerable movement. The caudal horn, or tail, can be moved in a wide arc in the vertical plane; this movement has been variously considered as a means of locomotion, of bringing food materials to the mouth, or of disorganizing the contents of the host egg. In *M. basalis*, the ring of long hairs on the abdomen, which normally lie flat upon the surface, can be raised perpendicularly, and a locomotory function is ascribed to them. Parasitized host eggs having a transparent chorion show a distinct undulatory movement of the fluid contents reminiscent of that seen in leaf-hopper eggs containing mymarid larvae.

Pupation takes place with the head usually at the anterior end of the host egg; and emergence, in the case of parasites in hemipterous eggs, is through an irregular hole in the operculum. The adults of *P. beneficiens* emerge largely during the early morning hours, whereas those of *E. benefica* do so during the late afternoon and early evening. This is the reverse of what would normally be expected; for the adults of *P. beneficiens* are nocturnal in habit, and those of *Eumicrosoma* are diurnal.

Mention has been made of species of *Limnodytes* and *Tiphodytes* parasitic in *Gerris* eggs. These eggs are deposited upon foliage beneath

the surface of the water; it is consequently necessary for the parasites to be capable of locomotion in this medium. They swim readily, using both the wings and legs, in contrast to certain other groups of aquatic Hymenoptera which use only the legs and find the host by crawling down plant stems, partly submerged stones, etc.

Reproductive Capacity.—The reproductive capacity of the Scelionidae is relatively low. The maximum is indicated for *Scelio fulgidus*, in which an average of 234 eggs was found in the ovaries of gravid females. In rearing tests, *Phanurus beneficiens* produced an average of 143 progeny, with a maximum of 275 from a single female. An average of only 22 eggs was found in the ovaries of *Eumicrosoma benefica*, and 54 was the largest number deposited by a single female. The ovaries of *Telenomus ulyetti* consist of only four ovarioles each, indicating a low reproductive capacity. At emergence, 6 to 14 fully mature eggs are found either in the uterus or ready to descend from the oviducts, and the individual egg production was found to average only 55. There is no difference between mated and unmated females of the Scelionidae in so far as oviposition activities or reproductive capacity are concerned, with the exception of *Eumicrosoma benefica*, the virgin females of which are said to deposit fewer eggs than do the mated females.

The initial batch of eggs is fully formed in the reproductive system of the female and ready for deposition at the time of emergence from the host egg. This appears to be true in the great majority of true egg parasites among the Chalcidoidea and Serphoidea, and their complete food requirements appear to be fully met by the contents of the host egg. In no species of the family have the females been observed to feed at the ovipositor puncture hole, and some are said not to feed at all during adult life.

With few exceptions, the Scelionidae are solitary parasites, only a single individual attaining maturity in each host egg. Five or six *T. nigrocoxalis* Ashm. are produced in each egg of *Brassolis saphorae* L., and a maximum of 16 is recorded for *T. fariai* in *Triatoma*. The solitary species deposit only a single egg at each insertion of the ovipositor, whereas the gregarious species deposit the full complement at one insertion.

In all species for which figures are available, the sex ratio shows a preponderance of females, ranging up to 10 to 1 in *P. beneficiens* in Java. The ratio of this species in Japan was found to be 2 to 1, though with males developing abundantly from the first and last eggs laid by the females. Parthenogenetic reproduction, in the few species tested, results in male progeny only. Costa Lima states that the males of *T. fariai* that are produced parthenogenetically differ markedly in size from those from mated females.

Life Cycle.—Under optimum conditions, the minimum duration of the life cycle is comparatively short, ranging in most species from 8 to 15 days, of which half to two-thirds is passed in the pupal stage. These species have a considerable number of generations each year, *E. benefica*, for example, having eight or nine during the season, resulting in the development of four or five successive generations in the eggs of a single host brood. *Rielia*, which attacks single-brooded hosts, has only a single annual generation, and the same is true of some species of several other genera.

P. beneficiens passes the winter in the adult stage in clumps of dry grass and other sheltered places. The majority of species that attack hosts overwintering as eggs appear to hibernate as first-instar larvae within them. In Australia, *S. fulgidus*, which is able to complete its cycle in four to five weeks, may persist for long periods in the adult form within the egg, a diapause induced by arid conditions, and emergence then takes place as soon as the soil is moistened.

IMMATURE STAGES

The eggs of the species of Scelionidae that have been described are of a uniform type, all being stalked, with the main body ovate to spindle-shaped and the tapering or tubular anterior stalk ranging in length from ½ to 1½ times that of the main body. The eggs of *Scelio* are slender, with the line of demarcation between the stalk and main body not distinct, and that of *S. pembertoni* has a small pedicel at the posterior end, also. There is an increase in size during incubation, as a result of which the stalk disappears.

The first-instar larva of the family is "teleaform," so-called from the larva of *Tiphodytes* (*Teleas* sp.) described and figured by Ganin (1869). It is characterized by a complete lack of segmentation but with the body divided by a sharp constriction into two more or less equal portions. There is a difference of opinion as to the parts that constitute the anterior portion. Henriksen, Bakkendorf (1934), and Pagden (1934) consider that it represents the head alone, whereas Noble and Kamal term it the cephalothorax, made up of the head and the three thoracic segments. This latter interpretation is more probably correct. The mandibles of all species are external, widely spaced, exceedingly large, curved, and sharply pointed and may be either heavily sclerotized or fleshy and unsclerotized. In *Phanurus* sp. dissected from eggs of *Chrysopa* in Japan, there are no other evident structures or organs on the cephalothorax, whereas in several other species of the family various head structures are well-developed. The antennal processes of *Scelio fulgidus* (Fig. 113*E*) and *S. pembertoni* are large and conical, are widely spaced, and arise immediately above the bases of the mandibles. In a number of species, there is a large, fleshy lobe or process on the median ventral line of the cephalothorax, below or behind the mandibles. This is highly developed in the genus *Scelio* (Fig. 113*I*) and has been considered the labium by several authors.

The abdomen is more or less globular in form and terminates in a caudoventral horn, or tail, which may be fleshy and of irregular form or heavily sclerotized, sickle-like, and terminating in a sharp point. In some species, there are one or two supplementary lobes at the base of the tail. The fleshy type of tail is usually spined dorsally and on the distal portion and is occasionally bifurcate at the tip.

In *Eumicrosoma, Telenomus, Scelio, Phanurus, and Microphanurus,* and probably in other genera also, there is a partial or complete transverse ring of long hairs near the anterior margin of the abdomen. These hairs vary considerably in number and distribution. In *E. benefica* (Fig. 113*B*), they occur upon the sides only, whereas in others the ring is complete and it is double in several species of *Phanurus*. The abdominal hairs of *Teleas* sp. (Fig. 113*C*, *D*) figured by Ayers (1884), *Limnodytes*, and *Tiphodytes* are in distinct tufts upon the summits of a pair of fleshy lobes situated at the lateroventral margins on the anterior portion of the abdomen. Marchal (1900) illustrates them in that arrangement in *T. gerriphagus* Marchal, whereas Martin (1928), dealing with the same species, shows the hairs in a transverse row.

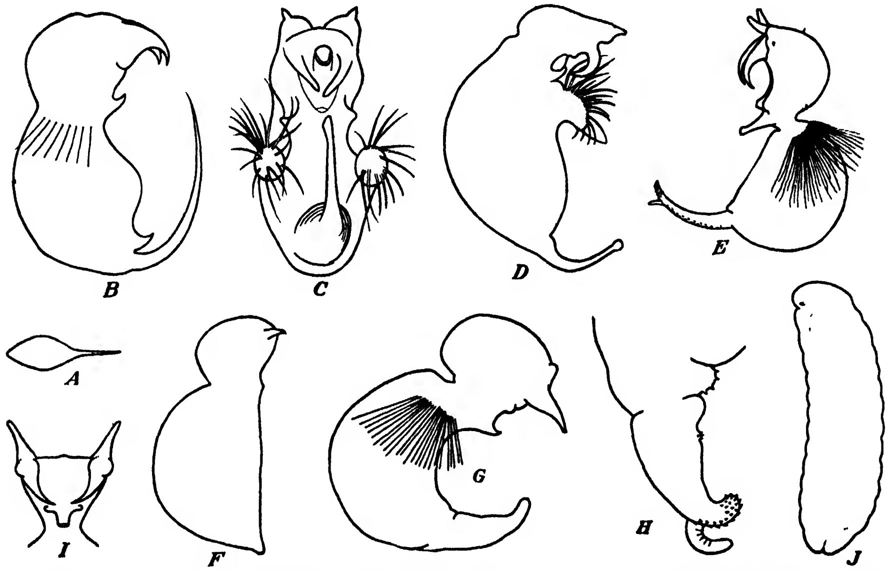


FIG. 113.—Immature stages of the Scelionidae. *A*, the egg of *Eumicrosoma benefica* Gahan; *B*, first-instar larva of same (*from McCulloch and Yuasa*, 1915); *C* and *D*, first-instar larva of *Teleas* sp., ventral and lateral views (*after Ayers*, 1884); *E*, first-instar larva of *Scelio fulgidus* Cwf. (*from Noble*, 1935); *F* and *G*, phases of the first-instar larva of *Rielia manticida* Kieff.; *H*, posterior portion of abdomen of same (*from Chopard*, 1923); *I*, head of first-instar larva of *Scelio pembertoni* Timb. (*from Pemberton*, 1933); *J*, second-instar larva of *Phanurus angustatus* Thom. (*from Bakkendorf*, 1934).

Chopard (1923) figures several supposed developmental phases of the first-instar larva of *Rielia manticida* in the eggs of Mantidae. The first (Fig. 113*F*), secured from host eggs in April, is of simple form, with the abdomen lacking the band of hairs and the tail. Those found in May show a lateroventral tuft of short hairs, and the tip of the abdomen is produced into a broadly conical tail. The form found in June and July (Fig. 113*G*) has the lateral abdominal hairs well-developed and the tail further enlarged (Fig. 113*H*). The author is inclined to consider the latter to be the second instar. It is, however, identical in general characters with the first-instar larva of various other species.

The second-instar larva has been described in only a few species. That of *T. gerriphagus* figured by Martin is irregularly ovoid in form, with the mandibles still large and a small hook-like caudal horn. Immediately above the mandibles are two plate-like thickenings of the integument, separated by a median depression. The abdominal

hairs are present in groups of five or six in a band across the dorsum and sides. None of these characters was found in all of the specimens examined, and the true form of the second instar is consequently still in doubt. That of *M. basalis* is very robust, with the segmentation indistinct; the mandibles are small and simple. There are no integumentary spines or setae, and the caudal horn is lacking. The second-instar larvae of *T. ulyetti* and *Phanurus angustatus* Thom. (Fig 113*J*) are cylindrical and distinctly segmented, but otherwise similar to that of *M. basalis*. Neither the first- nor second-instar larva of any species has been found to possess a tracheal system or spiracles.

The third-instar larva of *T. ulyetti* is similar in form to the second but may be readily distinguished by the presence of nine pairs of spiracles, situated on the last two thoracic and the first seven abdominal segments. Kamal mentions that only the two pairs of thoracic spiracles are functional in *M. basalis*, the following seven being minute and closed. The integument of the abdomen bears numerous small tubercles at the lateroventral margins, which extend across the venter on the posterior segments. This species and *S. fulgidus* are grayish-green in color.

The mature larva of *Cacus oecanthi* Riley bears a pair of rounded protuberances laterally on each body segment except the last, and the second to seventh segments also have a pair of prominent tubercles dorsally (Parrott and Fulton, 1914).

In a number of species, only two larval instars are mentioned, this being due presumably to the marked similarity of the second and third. The larva of *P. angustatus* described and figured as the second and last instar (Bakkendorf, 1934) is probably the true second, as judged by the lack of a respiratory system.

CALLICERATIDAE

The family Calliceratidae is relatively small, and the host preferences and habits of only a few species are known. They have been reared from Lepidoptera, Diptera, Coleoptera, Hymenoptera, and Homoptera, though the exact relationship has been determined in only a few instances. They are perhaps most generally encountered as secondary external parasites of Aphididae and dactylopine Coccidae through various braconid and chalcidoid primaries. *Calliceras abnormis* Perk. attacks the mature larvae of Dryinidae in their cocoons in Hawaii, and *Lygocerus semiramosus* Kieff. is a secondary parasite of Chermidae through Encyrtidae in India.

BIOLOGY AND HABITS

L. cameroni Kieff. (Haviland, 1920) is a secondary parasite of aphids through *Aphidius* spp. It attacks the mature larvae and at times the early pupae of *Aphidius* and occasionally develops upon corresponding stages of its own species. It is solitary and external in habit. Oviposition takes place only after the body contents of the aphid have been completely consumed by *Aphidius* and only the shell remains, which is lined with silk by the mature larva of the primary parasite. The female may either stand on the aphid body during oviposition or insert the ovipositor by a backward thrust. The egg is placed upon the dorsum of the body of the *Aphidius* larva or pupa. The meconium is cast by

the prepupa and is found as a single black, spherical mass lying in the mid-ventral curve of the pupa.

The cycle from egg to adult is complete in 21 to 24 days, of which the egg, larval, and pupal stages require 1, 6 to 7, and 14 to 16 days, respectively. The number of eggs deposited by a female was estimated not to exceed 25. The sex ratio is approximately 1.5 to 1, the females predominating.

The observations by Spencer (1926) on *L. niger* How. have shown that the host preferences and habits are similar to those given for *L. cameroni*. In this species, also, it was found that development takes place occasionally upon its own larvae. The egg is placed somewhat ventrally, rather than dorsally, upon the *Aphidius* larva or pupa. The body of the

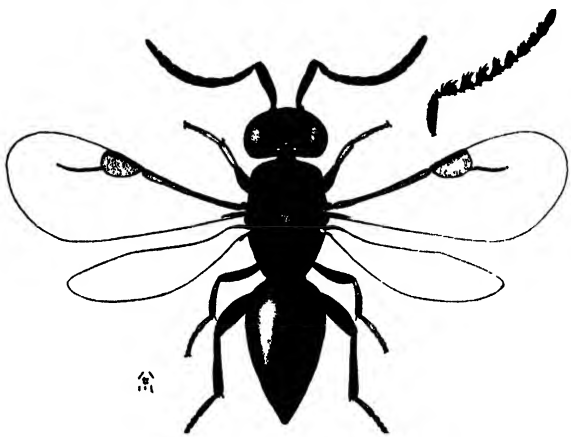


FIG. 114.—The adult female of *Lygocerus* sp., with antenna of the male. (Original.)

pupa is curved ventrally into a semicircle, and the single meconial pellet lies at the middle of the curve and is encircled by the antennae for three-fourths of its circumference. The cycle from egg to adult is complete in an average of 14 days. Parthenogenetic reproduction results in male progeny only.

The genus *Lygocerus* is known to be hyperparasitic upon mealybugs, also. *Lygocerus* sp. (Fig. 114) is a secondary parasite of *Pseudococcus* sp., through the encyrtid, *Clausenia purpurea* Ishii, in Japan. Attack is limited to the pupae, and it was not possible to secure oviposition on mature larvae. Because of the ellipsoidal form of the host cell, the pupa is fully extended, rather than curved as described for *L. cameroni*, and the single meconial pellet lies at the tip of the abdomen. The female of an undetermined species of *Lygocerus* is stated by Withycombe (1924*a*) to bite a hole in the cocoon of *Conwentzia psociformis* Curt. before depositing its egg.

The conical process upon the last abdominal segment of the larva of *L. cameroni*, which is present in other species of the genus, also, is believed by Haviland to have a locomotory function. Although there appears to be no need for such an adaptation in the confined quarters that the larva occupies, yet the exceptional mobility of the posterior portion of the body, observed in *Lygocerus* sp., supports this assumption. The movements of the tapering abdominal end of the body bring to mind those of the head and thorax of a syrphid larva when in search of food.

Kamel (1939) has given an account of his observations on the biology and habits of representatives of another genus of the family, *Conostigmus*, of which the species *C. zaglouli* Kamal and *C. timberlakei* Kamal were reared from puparia of Syrphidae in California. They are gregarious external parasites upon the pupa within the puparium. The eggs are deposited upon the integument of the newly formed pupa and hatch in 2 days. The larval period is relatively long, covering about 24 days, and the pupal period is 6 to 8 days. The cycle from egg to adult thus requires slightly more than one month. Under adverse conditions, the mature larvae of *C. zaglouli* may go into diapause for several months. The meconium is in the form of a large number of minute pellets rather than a single spherical mass such as is voided by *Lygocerus*. A maximum of 33 individuals of this species was reared from a single puparium.

The limited information available regarding the host relationships indicates that most if not all members of the family develop externally, though within the cocoon, puparium, or dead body of the primary or secondary host. No instance is known of attack upon naked larvae or pupae.

IMMATURE STAGES

The egg and larval instars of several species of *Lygocerus* and *Conostigmus* have been observed and described. In *Lygocerus*, four larval instars are recorded for *L. cameroni*, *L. niger*, and *Lygocerus* sp. from Japan, with some evidence presented that an additional instar may intervene between those described as the first and second. Kamal, however, found only three instars in *C. zaglouli* and *C. timberlakei*.

The egg of *L. cameroni* is elliptical in form, 0.25 mm. in length, and white in color, with a minute protuberance at one end, and the chorion bears minute longitudinal striations. That of *Lygocerus* sp. (Fig. 115*A*) is similar, though the nipple-like protuberance at the posterior end is considerably narrowed. In *L. niger*, there is a similar protuberance at the anterior pole, also.

The first-instar larvae of *L. cameroni* and *Lygocerus* sp. (Fig. 115*B*) are similar in form and have relatively large, rounded heads, followed by 12 body segments, with the greatest width occurring in the anterior abdominal region. The mandibles are minute and slender and are adapted for penetrating only a delicate host skin. The integument bears no sensory setae or cuticular spines. There are two pairs of spiracles, one situated on the intersegmental membrane separating the first two thoracic segments, or at the anterior margin of the second, and another on the first abdominal segment. The larva of *C. timberlakei* is distinguished by the size and form of the last

abdominal segment, which equals the four preceding segments in length and is deflected ventrad. No mention is made of the respiratory system.

The second-instar larva of *L. cameroni* is distinguished from the first by the possession of an additional body segment and four pairs of spiracles, these being situated at the anterior margin of the second thoracic and on the third thoracic and the first two abdominal segments.

The third-instar larva of *L. cameroni* is more robust than the second, being somewhat globose, with the head markedly ventral in position. There are seven pairs of spiracles, the first being situated at the posterior margin of the first thoracic segment and the following ones on the third thoracic and first five abdominal segments. Spiracular branches may also be found in the second thoracic and the sixth abdominal segments. The third-instar larva of *Lygocerus* sp. (Fig. 115*C*) differs from the above in the more elongate form of the body and the presence of transverse rows of conical protuberances dorsally and laterally upon all body segments except the last. The caudal segment is somewhat irregularly bilobed transversely.

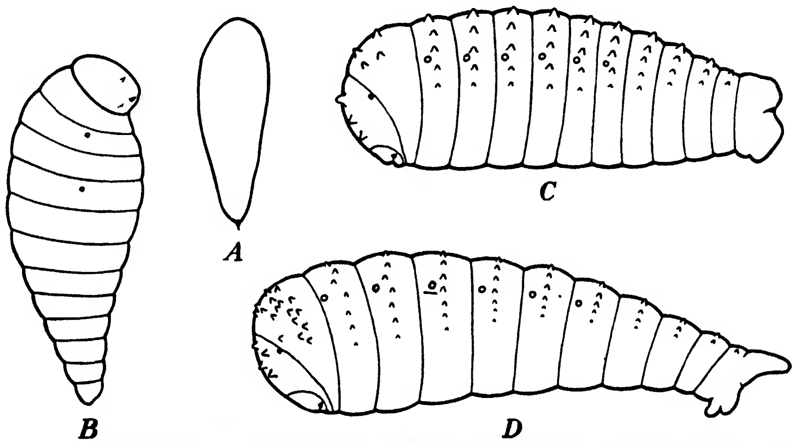


FIG. 115.—Immature stages of *Lygocerus* sp., a secondary parasite of *Pseudococcus* in Japan. *A*, the egg; *B*, *C* and *D*, first-, third- and fourth-instar larvae. (Original.)

The mature larvae of *L. cameroni*, *L. niger*, and *Lygocerus* sp. (Fig. 115*D*) are similar in all principal characters. The body is robust, broadest in the thoracic region, and curved or straight according to the cell that it occupies. The head is relatively small, with simple mandibles. In all these species, the last abdominal segment is transversely bilobed, the dorsal lobe being distinctly conical in form. The thoracic and all abdominal segments except the last bear conical papillae or tubercles on the dorsum and sides, which are arranged in transverse rows in *L. niger* and *Lygocerus* sp, and are scattered in *L. cameroni*. In the latter species, they occur also upon the conical process of the last abdominal segment. There are seven pairs of spiracles, situated at the posterior margin of the first thoracic segment and on the third thoracic and first five abdominal segments. In *Lygocerus* sp., these are markedly dorsal in position, and the pair on the third thoracic segment is much the largest.

The mature larva of *Conostigmus*, which is stated by Kamal to be the third instar, lacks the principal characters that readily distinguish *Lygocerus*. The conical integumentary papillae and the conical process on the last abdominal segment are lacking. The head is exceptionally large and hemispherical, and the last abdominal segment is longer than those preceding it and smoothly rounded. In *C. zaglouli*, each abdominal

segment, except the last, bears a sclerotized ring, which is much heavier ventrally than on the dorsum. There are eight pairs of large spiracles, whereas *C. timberlakei* has only six, situated on the first thoracic and the first five abdominal segments.

DIAPRIIDAE

The relatively few species of Diapriidae of which the host preferences and relationships have been determined are internal parasites of the immature stages of Diptera. The known species of *Galesus* and most *Trichopria* oviposit into the puparium.

Galesus silvestrii Kieff. (Fig. 116) is a West African parasite of the pupae of various species of fruit flies of the family Trypetidae, and an

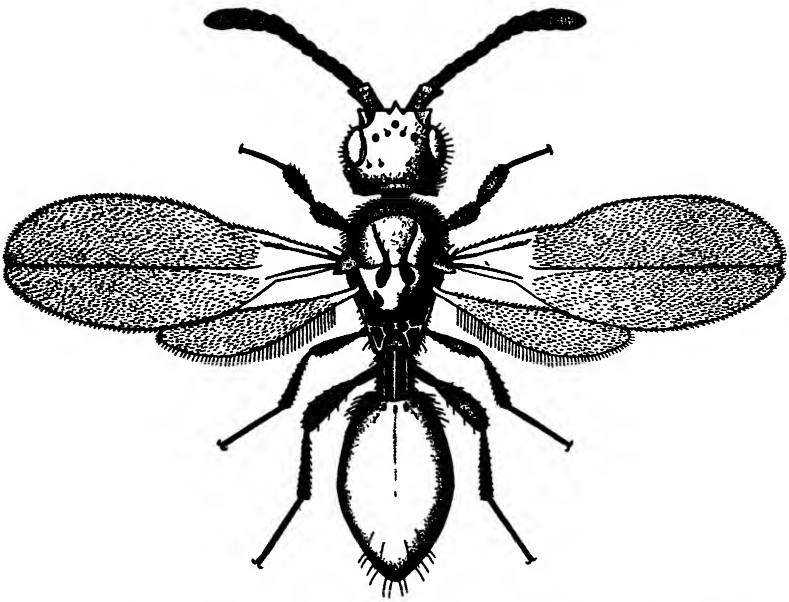


FIG. 116.—The adult female of *Galesus silvestrii* Kieff. (*Redrawn, after Silvestri*, 1914.)

unsuccessful attempt was made to establish it in Hawaii in 1913. Experimental studies by Pemberton and Willard (1918) indicate that it develops quite as readily as a secondary parasite, through various *Opius* species, as in the primary role.

In oviposition, the female stands upon the puparium, with the body somewhat arched, and inserts the ovipositor nearly perpendicularly. The egg, which is placed within the body of the pupa, is subelliptical in form, has both ends smoothly rounded, with the chorion smooth, and measures 0.36 mm. in length. In case the puparium already contains an *Opius* larva, the egg is invariably placed within its body rather than merely in the body of the fruit-fly pupa. This is true also when *Tetras-*

tichus larvae are present, even though these are very small, measuring only twice the length of the *Galesus* egg. Development to maturity may take place in these larvae, though the resulting adults are dwarfed, being only 1.5 mm. in length.

The first-instar larva (Fig. 117) is robust in form and is of the mandibulate type. The head is very large, somewhat flattened, and heavily sclerotized and bears a pair of very large curved mandibles. There are 12 body segments; the last segment bears a pair of terminal lobes which carry a number of setae. Aside from these there are no integumentary spines or setae.

The second-instar larva (Fig. 117) lacks the large, heavily sclerotized head of the preceding instar and is of normal form. Neither this nor the first instar possesses a tracheal system. The supposed third- and final-instar larva is elongate in form, with 12 body segments, and its distinguishing feature is the possession of a complete tracheal system with three pairs of large spiracles on the thoracic segments. The contents of the host puparium are entirely consumed. The meconium is cast by the prepupa, and after the final molt the pupa lies with its head at the anterior end of the puparium. Emergence of the adult is effected by pushing off the dorsocephalic cap of the puparium; because of this habit, empty puparia which have yielded *Galesus* are not readily distinguishable from those which have produced flies.

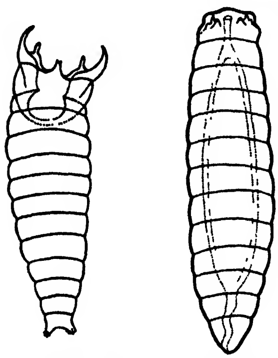


FIG. 117.—The first- (at left) and second-instar larvae of *Galesus* silvestrii Kieff. (*From Pemberton and Willard*, 1918.)

The adults fly very little and spend the greater portion of their lives on or in the soil, in search of host puparia.

The cycle from egg to adult is complete in 25 to 32 days. Unmated females produce male progeny only.

Trichopria hirticollis Ashm. (Roberts, 1935) is a gregarious internal parasite of the pupae of *Sarcophaga* and other blowflies. A maximum of 44 individuals was reared from a single puparium. The life cycle is completed in 25 to 30 days. *Diapria conica* F. develops similarly in the puparia of the syrphid, *Eristalis tenax* L. (Sanders, 1911). Young puparia are preferred for oviposition, and the ovipositor is usually inserted immediately behind the pupal cornicles. The ovipositor remains inserted for one to three hours, and the full complement of mature eggs is deposited upon the one host. An average of 35 individuals develops in each puparium. Unmated females produce only male progeny, but most broods contain a preponderance of females.

T. stratiomyiae Kieff. (Cros, 1935), parasitic in *Stratiomyia anubis* Wied. in Algeria, departs from the normal habit of the family by attacking the larvae rather than the puparia. The ovipositor is inserted by a backward thrust through the thin intersegmental membrane. Death of the host takes place without the pupal stage being attained. A maximum of 293 individuals has been reared from a single host. Mating takes place outside the body of the host immediately following emergence.

SERPHIDAE

Biological studies have been made upon only a very few species of the family. So far as known, they are solitary or gregarious parasites of the larvae of various Coleoptera such as the Staphylinidae, Carabidae, Elateridae, and Coccinellidae; a number of species are recorded from Diptera. *Serphus ater* Nees has been reared as a parasite of the centipede, *Lithobius* sp. In view of the attack upon the groups of predaceous beetles mentioned above, it is uncertain whether the family is to be considered predominantly beneficial or harmful. None of the species is sufficiently abundant to be of any appreciable consequence in either capacity.

BIOLOGY AND HABITS

Several partial life-history studies have been made, the most informative being that of Eastham (1929) on *Phaenoserphus viator* Hal., a gregarious internal parasite of the larvae of various Carabidae in Europe. There is presumed to be a single annual generation upon *Pterostichus niger* Schall., and the adults appear in the field during August and September.

Development of the larva is very slow during the feeding and hibernating periods of the host, and the first-instar larva persists until the host larva approaches the time for pupation in the spring or early summer. Growth of the parasite then becomes rapid, and the body contents of the host are almost completely consumed. When feeding is complete, the larvae, to the number of 30 or more, emerge from the body in an orderly way. Just prior to breaking through the skin, they are all oriented longitudinally, with the heads directed caudad. The individual ruptures in the host integument are made in transverse rows of three or four, always ventrally and intersegmentally. About three-fourths of the body of the parasite is extruded from the wound, and the caudal portion remains within it and serves to hold the prepupa and later the pupa in position. The last larval molt takes place immediately after emergence is effected. No cocoon is formed. The external prepupal stage is relatively long, requiring 7 to 10 days, and the pupal stage covers about two weeks.

Raynaud (1935) has made some observations upon *Phaenoserphus viator* as a parasite of the larvae of *Carabus* in Europe. The observed habits were similar to those described above, though it was assumed that the winter is passed in the egg stage.

An account of the habits of *Paracodrus apterogynus* Hal. as a parasite of the larva of *Agriotes* has been given by Zolk (1924). Development is

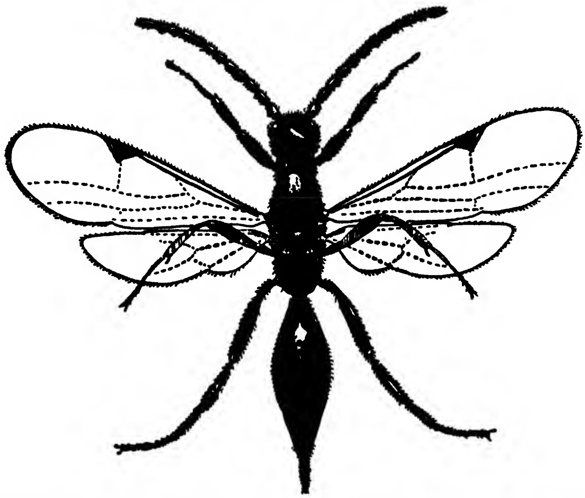


FIG. 118.—The adult female of *Exallonyx philonthiphagus* Will. (*From Williams*, 1932.)

FIG. 119.—A pupa of *Exallonyx philonthiphagus* Will., with its posterior abdominal segments embedded in the body of the host larva. (*From Williams*, 1932.)

similar to that of *Phaenoserphus*, and the emergence habit is identical, though if the number is not excessive only two individuals emerge from each intersegmental area. From 14 to 52 reach maturity in a single host. Gravid females contain up to 170 eggs.

Exallonyx philonthiphagus Williams (Fig. 118) is a solitary internal parasite of the mature larvae of *Philonthus turbidus* Erich. in Hawaii (Williams, 1932). The fully fed larva emerges from the host body through an aperture in the fifth or sixth abdominal segment ventrally. The pupa lies with its venter to that of the host, and the head is directed

forward. In the case of female pupae, only the tip of the abdomen remains within the host body (Fig. 119), whereas in the males the head and thorax only are external.

Observations have been made on an undetermined species of the family that is a solitary parasite of *Scymnus* larvae in Japan. Oviposition takes place in first- and early second-instar larvae and is accomplished by bringing the abdomen forward beneath the body and inserting it by a rapid thrust, somewhat ventrally, in the mid-abdominal region of the host. Larval development is rapid, and feeding is completed at the time the host larva has attached itself to the leaf or bark preparatory to pupation. At this time, the parasite larva lies with its head at the caudal end of the body. The body contents are not entirely consumed, and feeding has apparently been only upon the fluid or semifluid contents. Emergence from the host is accomplished not by cutting the integument with the mandibles, but in the following interesting manner. The head of the mature larva is pressed against the skin ventrally near the caudal end of the body, and then, by rhythmic pulsations over a period of several hours, it is forced outward more and more until a break occurs. As soon as the greater portion of the body is free, the last larval exuviae is cast and the pupa then lies venter to venter with its host and with the tip of the abdomen curved ventrally, enveloped in the last larval exuviae, and still embedded in the host body. The time required to effect complete emergence is about 12 hours, and a further 36 hours elapses before pupation. The entire life cycle is complete in about 20 days.

From the incomplete data available regarding the habits of the family, it appears that there is a considerable uniformity in the manner of development of the larvae, their emergence from the body of the host and the peculiar position assumed by the pupa beneath the host body.

IMMATURE STAGES

The information on the egg and the larval instars of the family is incomplete The egg of the species attacking *Scymnus* larvae in Japan (Fig. 120*A*) is somewhat cylindrical, but slightly wider at the anterior end; the poles are smoothly rounded; and it measures 0.2 mm. in length and 0.06 mm. in width. The ovarian egg of *Paracodrus* observed by Zolk is somewhat elongate and measures 0.14 to 0.16 mm. in length.

The first-instar larva from *Scymnus* (Fig. 120*B*) is polypodeiform, and the large paired ventral processes occur on the first thoracic and the first four abdominal segments. The head is large and heavily sclerotized, bears heavy falcate mandibles, and is, consequently, quite similar to that of mandibulate-type larvae. The body is widest at the juncture of the thorax and abdomen and narrows appreciably to the seventh segment, following which is the apparently four-segmented tail, which is directed dorsad almost at right angles to the body axis. The integument bears no spines or setae and is much more delicate on the tail than on the remainder of the body. There is no evidence of a tracheal system or spiracles.

The larva of *Phaenoserphus viator* described by Eastham is similar to the above in the essential characters, except that 10 body segments are recognizable, of which the last is much the longest and in older specimens is seen to comprise 4 segments, making a total of 13. The fleshy paired ventral processes occur on the second and third thoracic and the first six abdominal segments and are considered to be vestigial organs. The distal portion of the tail bears vertical fin-like projections both dorsally and ventrally.

The following instars are of normal form, lacking the large head, the paired appendages, and the tail. The third instar of *P. viator* may be recognized by the presence of 8 pairs of nonfunctional spiracles, whereas the fourth instar has 10 pairs, situated on the second and third thoracic and the first eight abdominal segments. Both of these instars have the labrum projecting over the mouth in the form of a rounded beak. There are no integumentary spines or setae.

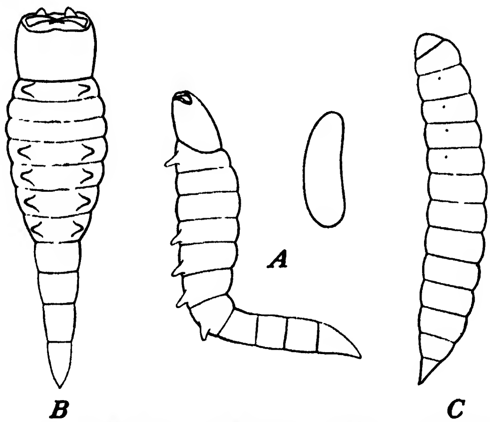


FIG. 120.—The immature stages of a serphid parasite of *Scymnus* larvae in Japan. *A*, the egg; *B*, first-instar larva, ventral and lateral views; *C*, mature larva, lateral view. (Original.)

The mature larva of the Japanese species (Fig. 120*C*) is slender and cylindrical, with 13 body segments, of which the last is small and tapers to a point. The tracheal system has the same number and arrangement of spiracles as occurs in *P. viator*.

The pupae of all species that have been studied have the posterior portion of the abdomen strongly curved ventrally.

HELORIDAE

The family Heloridae comprises a very small number of species contained principally in the genus *Helorus*. Very few records are available regarding the host preferences of the genus, which appear, however, to be limited to the Chrysopidae. The species of known habit develop as internal parasites of lacewing larvae, and adult emergence is from the cocoon. Aside from the few published host records, the only knowledge available regarding the biology and habits of the group is the extended study of *H. paradoxus* Prov. recently made by Clancy (unpublished), who has kindly permitted the inclusion of the following summary.

BIOLOGY AND HABITS

H. paradoxus is very largely restricted to *Chrysopa majescula* Banks, though several other species of the genus are present in the same habitat. The females have a preoviposition period of two to eight days, after which the host larvae in any stage of development are attacked. The abdomen is brought forward beneath the body, and the ovipositor is inserted into the lateral or lateroventral region of the host body, usually the abdomen. After insertion is effected, the female folds her legs and may be dragged about for a time by the excited host. Only a single

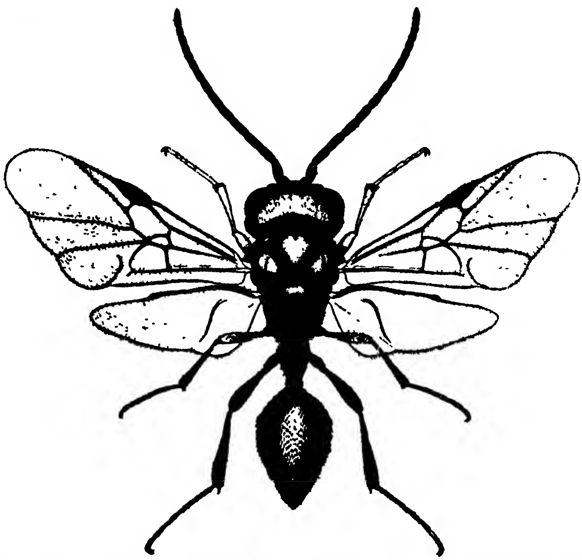


FIG. 121.—The adult female of *Helorus paradoxus* Prov. (*Drawing by D. W. Clancy.*)

egg is laid at each insertion. Adult life may extend to four to six weeks; during this period, approximately 50 eggs are laid, usually at the rate of 1 or 2 each day.

The egg is free-floating in the body fluids of the host, and it increases considerably in size during incubation. The embryo lies curled within the shell with the head at the micropylar end (Fig. 122*B*). Hatching takes place in a minimum of 2 days after deposition of the egg. The duration of the larval period, particularly the first stage, is variable, for the first molt does not take place until the host cocoon is spun and the prepupal stage attained. In hosts that carry over until the second year, the parasite persists in the first stage through that extended period. When oviposition is in nearly mature host larvae and under summer conditions, the stage covers only 3 to 6 days. Soon after the first molt, the host body fluids become filled with opaque white bodies, which are

spherical in outline, and as these increase in number there is a corresponding decrease in the fat bodies and softer tissues. It appears that the parasite larva must secrete some enzyme which causes the breakdown of the host tissues. All movement by the host ceases about the middle of the second larval stage of the parasite, and death takes place coincident with the second molt. The second stage covers 2½ to 3 days. Feeding is very extensive after the second molt, and the body contents of the host are completely consumed within 2 days. The orientation of the body is the reverse of that of the host. After remaining in the empty skin for several days, the larva emerges from a point near the posterior end, and only the last four or five segments remain embedded in the wound (Fig. 122*F*). A further resting period ensues, and pupation then takes place. The tip of the abdomen of the pupa retains a light attachment to the host remains. The body is greatly curved to fit the outline of the host cocoon. The larval meconium is not voided until after the emergence of the adult. The pupal stage is complete in 8 to 12 days, thus giving a total of 22 to 40 days for the cycle from egg deposition to emergence, with an average of about 30 days. Several generations are produced each year, and hibernation takes place as a first-instar larva within the host larva in its cocoon.

On the basis of incomplete information, it appears that the females of *H. paradoxus* greatly outnumber the males.

IMMATURE STAGES

The early stages are known only in the case of *H. paradoxus*, and consequently no general description can be given for the family. It is noteworthy, however, that the instars here described bear a striking similarity to those of *Phaenoserphus* and *Paracodrus* of the Serphidae and of *Collyria* of the Braconidae.

The newly laid egg of *H. paradoxus* (Fig. 122*A*) is white, oblong in form, and slightly wider at the anterior end and bears a minute conical micropyle.

The first-instar larva (Fig. 122*C*) is elongate and polypodeiform, with 13 body segments, of which the posterior ones are indistinctly indicated. The head is heavily sclerotized and bears a peculiar oral "sac," which is structureless and transparent. Within this sac are the mandibles, which are large and heavily sclerotized. Each abdominal segment except the last bears a pair of large fleshy processes ventrally. Those of the caudal segments are of decreasing size. The last segment is drawn out into a short, ventrally curved tail. The respiratory system is vestigial and consists only of two short lateral trunks with a small number of simple branches but no commissures.

The second-instar larva (Fig. 122*D*) is unlike the preceding one; for it lacks the heavily sclerotized head capsule and the fleshy paired ventral processes, and the tail is greatly reduced. The mandibles appear to be entirely lacking. There are no cuticular spines or setae. The respiratory system comprises well-developed lateral trunks extending the length of the body, with spiracular spurs in many segments and extensive dorsal and ventral branches, but no commissures or spiracles.

The mature third-instar larva (Fig. 122*E*) is robust in form and is distinguished principally by the markings of the head. There is a peculiar dark-brown melanized

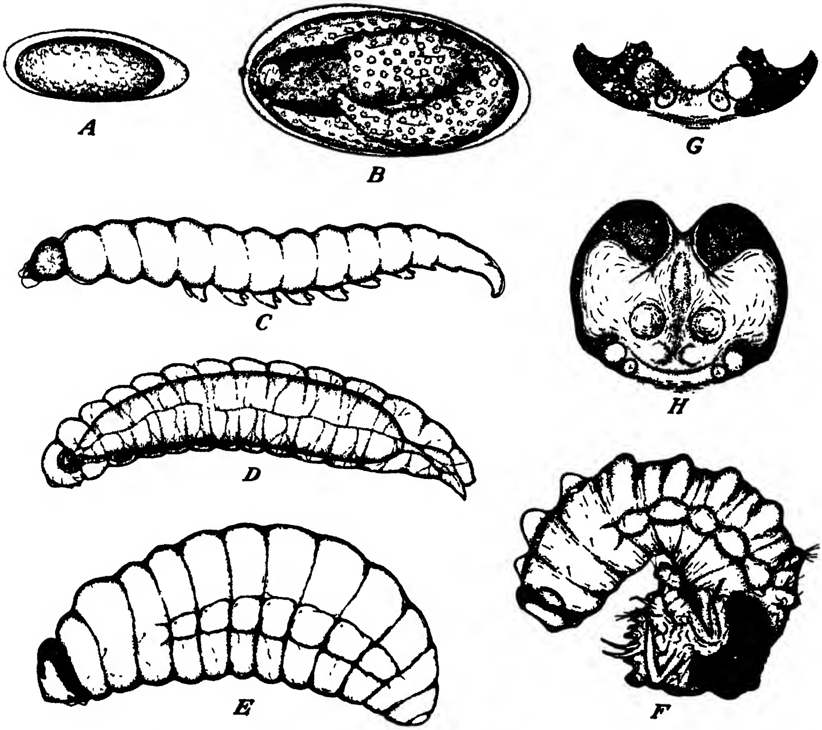


FIG. 122.—The immature stages of *Helorus paradoxus* Prov. *A*, newly laid egg; *B*, egg containing fully developed embryo, just before hatching; *C*, first-instar larva; *D*, second-instar larva; *E*, third-instar larva; *F*, mature larva with posterior segments of abdomen embedded in the host remains; *G*, mouth parts of mature larva; *H*, face of the mature larva. (*Drawings by D. W. Clancy.*)

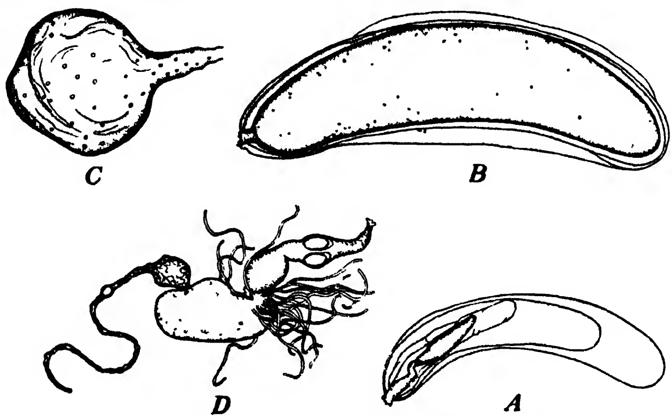


FIG. 123.—The peritrophic sacs of *Helorus paradoxus* Prov. *A*, the sac from the mid-gut of a second-instar larva; *B*, the same from a freshly molted third-instar larva; *C*, the same from a mature third-instar larva; *D*, the alimentary tract from a pupa, showing the reduced food mass in the mid-gut. (*Drawings by D. W. Clancy.*)

band (Fig. 122*H*) encircling the lateral posterior margins, which appears gradually and is apparently oxidative in nature. The mandibles are widely spaced and vestigial. Eight pairs of spiracles are present, these being situated near the anterior margins of the second and third thoracic and the first six abdominal segments. Blind spiracular stalks occur in the seventh and eighth abdominal segments. The posterior commissure is still absent in this instar.

In the second and third instars, there is a peculiar modification in the mid-gut, apparently not noted heretofore in parasitic larvae, consisting of a series of five membranous sacs, each within the next largest one, and connected by a definite cellular neck to the juncture of the fore- and mid-gut (Fig. 123). They are termed "peritrophic sacs" by Clancy and they increase greatly in size as larval development progresses. It has been determined that these sacs serve as a form of filter to abstract the excess moisture from the meconial mass, and the solid materials are then retained in the body until the emergence of the adult.

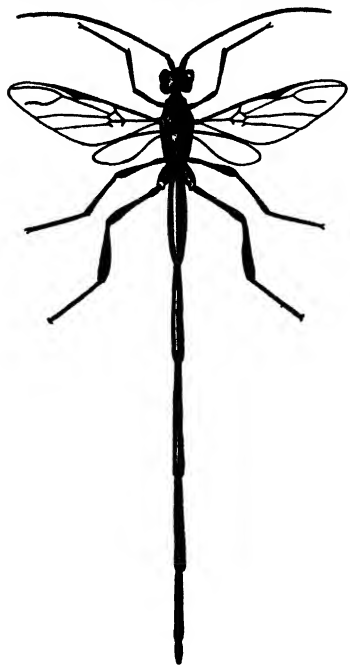


FIG. 124.—The adult female of *Pelecinus polyturator* Drury.

VANHORNIIDAE

The family is represented by a single North American genus and species, *Vanhornia eucnemidarum* Cwf., which has been reared from the cells of larvae of the coleopterous family Eucnemidae in decaying or sound wood (Crawford, 1909). Nothing is known regarding its habits or the form of the early larval instars.

PELECINIDAE

Only fragmentary information is available regarding the biology and habits of this family, and the few observations that have been made were upon *Pelecinus polyturator* Drury (Fig. 124) in North America. The adult female is 2 to 3 in. in length and of striking form, with the abdomen exceedingly long and slender and, in flight, carried in a characteristic curved position. The male is of normal form, with a club-shaped abdomen.

The parasitization of scarabaeid larvae by this parasite was first observed by S. A. Forbes in 1889, and rearings from similar hosts have been reported by several investigators since that time. In some instances, the host had attained the pupal stage before death. Development is internal, and pupation takes place outside the body of the host. The habitat of the adult females, however, is not that in which grubs of the phytophagous Scarabaeidae are commonly found. They are invariably associated with trees of some sort and are particularly numerous in cutover areas. It appears probable that the true hosts are coleopterous

larvae living in decaying wood and that attack upon scarabaeid larvae is only incidental. The adults appear in the field during July to September, and there is presumably a single generation each year.

In North America, the males of *P. polyturator* are exceedingly rare, leading to the belief that reproduction is normally unisexual. The neotropical varieties in collections are represented by numerous males, and these apparently represent geographical strains in which reproduction is bisexual (Brues, 1928).

CYNIPOIDEA

The superfamily Cynipoidea is known principally through its predominantly phytophagous habit, which is conspicuously evident because of the formation of galls of great variety in size and form upon the foliage and stems of many kinds of plants. These numerous species comprise the subfamily Cynipinae, which includes no parasitic forms. The parasitic representatives of the family that have been studied are of the subfamilies Ibaliinae, Figitinae, Eucoilinae, and Charipinae. Several minor subfamilies are also known to be parasitic, but little information is available regarding their host relationships. The Cynipinae, Ibaliinae, and Figitinae, the last including the Eucoilinae and Charipinae, are often given family rank.

All parasitic members of the family of which the habits are known develop internally in the immature stages of their hosts. The Ibaliinae are parasitic in the larvae of wood wasps of the genus *Sirex*, the Eucoilinae and Figitinae in larvae of Diptera; the Charipinae are hyperparasites of Aphididae through *Aphidius* and other Aphidiinae.

BIOLOGY AND HABITS

In the Ibaliinae, the one species that has been studied extensively is *Ibalia leucospoides* Hoch. of Europe, which is a parasite of *Sirex cyaneus* F. In recent years, it has been colonized and established in New Zealand. An extended account of the biology and habits of this species has been published by Chrystal (1930).

In attacking the host in its oviposition tunnels, the ovipositor of the parasite is inserted into the entrance of the tunnel and the stalked egg placed either in the egg of the host or in the newly hatched larva. Two to seven host eggs or larvae are present in each tunnel, and several may be parasitized at one insertion of the ovipositor. In some instances, the tip of the egg stalk remains fixed in the puncture in the integument. During incubation, there is an increase of three to eight times in both dimensions, and the volume increase is consequently very considerable.

The duration of the egg stage is extremely variable, ranging from six weeks to almost a year. Advanced embryos have been found three

to four weeks after deposition of the eggs. The trophamnion is very prominent and may envelop the first-instar larva for a considerable time, extending to almost one year. It is abandoned before the first molt but persists unchanged in form during the succeeding larval stages and consequently is not considered to have a nutritive function. The "polypodeiform" first-instar larva is considered by Chrystal to be "a relic of what was once an eruciform or active larval type."

Parasitism by *Ibalia* produces a pronounced effect on the feeding activities of the young *Sirex* larvae. During the first year, their tunnels are only half the length of those made by healthy larvae. One very characteristic feature of the tunnels of parasitized larvae is that they tend to turn toward the surface of the wood, a tendency evidenced in healthy individuals only at the end of larval development.

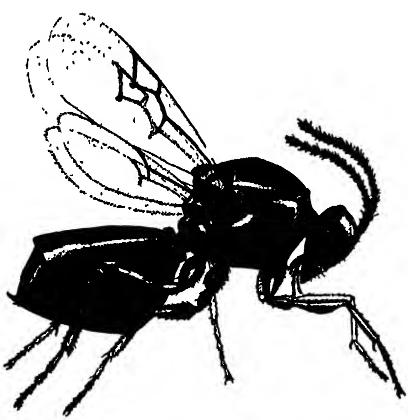


FIG. 125.—The adult female of *Psilodora* sp. (*From Roberts*, 1935.)

The third-instar larva emerges from the body of the host and completes its feeding externally. The body contents are completely consumed at this time, and there is, consequently, no feeding in the fourth stage. The second and third larval stages are comparatively short as compared with the egg and the first and fourth larval stages. The fourth stage may approach one year in duration. The pupal stage covers five to six weeks. The length of the entire cycle from egg to adult has not been definitely determined but is concluded to be not less than three years. All stages may be found in the field at any time of the year.

Emergence of the adults takes place from August onward. The males emerge first and may frequently be seen on the bark near the point where a female will soon emerge. An unusual habit in *Ibalia* is the frequent occurrence of mating while the female is in the act of oviposition.

The Eucoilinae are the best known of the parasitic Cynipoidea and are limited in their host preferences to the Diptera. Oviposition is in the early larval instars, and the adults emerge from the puparia.

Cothonaspis rapae Westw. is representative of the subfamily, and accounts of its biology and habits as a parasite of the cabbage maggot, *Hylemyia brassicae* Bouché, are given by James (1928) and Malchanova (1930). Only the first two larval instars of the host are subject to attack, and darkness is essential for oviposition, though the adults are diurnal

in habit. For this reason, maggots in the leaves and stem are probably immune. The parasite adults are attracted to the door of infested cabbage, and no attention is paid to free larvae or to those which have been transferred to a fresh plant.

The life cycle is complete in a period of about three months, of which incubation of the egg covers six days and the larval period about two months. Hibernation takes place in the mature larval stage. Two generations are produced each year.

Accounts have been given of the biology and habits of *Eucoila keilini* Kieff. (Keilin and Baume-Pluvinel, 1913) and of *Kleidotoma marshalli* Mshll. (James, 1928). The conspicuous ventral thoracic processes and the tail of the first-instar larva of *Eucoila* (Fig. 127*B*) are stated to be adaptive only and to serve in locomotion and respiration. James, on the contrary, could find no evidence of their use in locomotion by *Kleidotoma*. As in *Cothonaspis,* both these species have two generations annually.

Parasitized host puparia were found to be below normal size, and this effect appears to be consistent in all Diptera attacked by members of the family.

Roberts (1935) has made some observations on *Psilodora* sp., which attacks blowfly larvae inhabiting dung and carrion. The life cycle covers an average of 35 days under summer conditions; but there is tendency for the pupal period to be greatly prolonged, and some individuals remain in diapause for seven months. Hibernation takes place in the mature larval or prepupal stage in the host puparium. Parthenogenetic reproduction results in male progeny only.

The Figitinae, like the Eucoilinae, are solitary internal parasites of the larvae of Diptera and complete their development in the puparium. *Figites anthomyiarum* Bouché (James, 1928) attacks the larvae of various Diptera found in decaying meat. Oviposition takes place only in first- or second-instar larvae, and a preference is shown for those which have just hatched. A temporary paralysis is effected, which is of one or two minutes' duration. The initial stimulus for oviposition is undoubtedly provided by the decaying meat rather than by the maggots themselves.

Emergence of the adult takes place from the host puparium. The cycle from egg to adult covers a period of about 60 days under summer conditions, of which the egg, larval, and pupal stages cover 2 to 3, 38, and 20 days, respectively. There are two and possibly three generations each year, and the winter is passed in the mature larval stage in the host puparium.

The normal length of adult life is only eight to nine days. Feeding is mainly upon juices of the meat infested by the hosts. There is a preoviposition period of about two days, and an examination of the repro-

ductive system of gravid females reveals the presence of several hundred mature eggs, indicating a relatively high capacity.

Studies on the Charipinae have been made by Haviland (1921) and Spencer (1926). An undetermined species of *Charips* studied by Haviland is a solitary internal parasite of the late larval instars of *Aphidius ervi* Hal. in *Macrosiphum urticae* Kalt. and of other Aphidiinae in various aphids. Oviposition takes place most frequently in the third- or early fourth-instar *Aphidius* larva, though at times in the late second instar, and while the aphid host is still alive. The female mounts upon the back of the aphid, orients herself with the head toward that of the host, and inserts the ovipositor perpendicularly.

The trophic membrane surrounding the embryo usually disappears at the time of hatching of the egg, though occasionally it persists until after the first molt. The first-instar larva is usually found ventrally in the posterior or anterior third of the host body and between the nerve cord and the intestine. The last-instar larva emerges from the host through a break in the skin behind the head and completes its feeding externally. This ectoparasitic phase covers only about 12 hours.

The pupal stage covers 22 to 26 days, and emergence of the adult is effected by biting out an irregular hole dorsally in the host cocoon and the aphid skin. Adult life is relatively short, and feeding takes place upon honeydew and plant sap.

Spencer gives a brief account of *Charips brassicae* Ashm., the habits of which are similar to those given above. The first-instar larva is enveloped by the trophamnion, and feeding during the early stages is by diffusion through the thin integument. The aphidiine host is half-grown when first attacked and attains the pupal stage before death. Twenty-six days are required for the completion of the life cycle.

IMMATURE STAGES

The Egg.—The eggs of the parasitic members of the family are uniformly of the stalked type, with the stalk, which is situated at the anterior end, ranging in length from less than that of the main body, as in *Charips* sp. (Fig. 126*A*), to several times its length. That of *Figites anthomyiarum* (Fig. 128*A*) is elongate and somewhat constricted in the middle and has a stalk of about equal length. In *Eucoila keilini*, the stalk is twice the length of the egg body, and in *Ibalia leucospoides* it is about four times as long. The chorion is thin and transparent and without surface ornamentation.

First-instar Larva.—The known first-instar larvae of the family are of several distinct types. The "polypodeiform" larva of *I. leucospoides* (Fig. 127*A*) is unusually elongate, with a relatively large head, which is somewhat flattened dorsoventrally and provided with falcate mandibles. Of the 13 body segments, all except the last bear a pair of fleshy, finger-like processes ventrally, which are of uniform length. There are no integumentary spines or setae. The last abdominal segment is prolonged into a dorsally curved tail equal in length to the four preceding segments.

The first-instar larvae of the several genera of *Eucoilinae* that have been described are distinctive and readily recognized and have been designated as "eucoiliform."

The essential characters of this larval type that distinguish it from the polypodeiform are the long, paired, fleshy ventral processes on the thoracic segments only and an exceptionally long, tapering tail. In *Eucoila keilini* (Fig. 127*B*), the head is large and somewhat conical, and the body segmentation is indistinct. The fleshy thoracic processes are about half the length of the body and taper to a blunt point. The posterior segments of the abdomen are very much narrowed, being only very slightly wider than the base of the tail, and the tail itself is appreciably longer than the thoracic processes, is curved ventrally, and terminates in a sharp point. The segment immediately preceding the tail bears a fleshy conical lobe on the median ventral line. The integument of the posterior abdominal segments bears numerous short sclerotized spicules.

The larva of *Cothonaspis rapae* described by James and Malchanova is similar to that of *Eucoila*. There are at least seven distinct abdominal segments in addition to the two or more that make up the tail, and the latter organ is nearly as long as the entire body. There are a few setae upon the thoracic processes, and the distal third of the tail bears numerous spines.

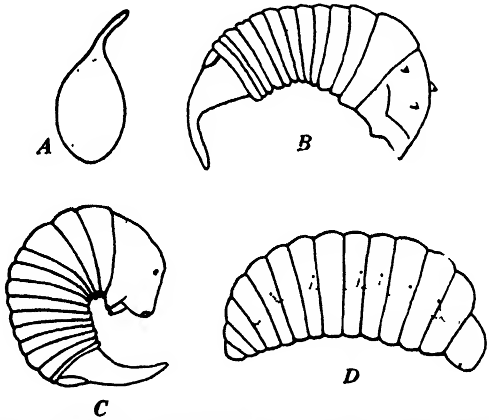


FIG. 126.—The immature stages of *Charips* sp. *A*, the egg; *B*, *C*, and *D*, first- and second-instar and mature larvae. (*From Haviland*, 1921.)

The eucoiliform larva of *Kleidotoma marshalli* figured and described by James has 12 apparent body segments, and the body is much more slender than that of *Eucoila* or of *Cothonaspis*. The head is large, with the mouth opening distinctly ventral. The fleshy thoracic processes are much shorter, being equal only to one segment in length, and they bear no setae. Stout setae are present on the distal portion of the tail. The anal opening is indicated on the dorsum of the eighth abdominal segment.

The first-instar larva of *Figites anthomyiarum* (Fig. 128*B*) is modified eucoiliform, the thoracic processes being even more reduced than in *Kleidotoma*, with the prothoracic pair only as long as wide, and the tail is short, almost cylindrical, and bluntly rounded rather than pointed at the tip. The segmentation is distinct, and the 12 body segments preceding the tail bear fleshy spines on the dorsum, these being largest in the mid-abdominal region.

In the Charipinae, the only first-instar larva thus far described is that of *Charips* sp. (Fig. 126*B*), by Haviland. This larva has few characters in common with other members of the family and must be considered as a modified caudate form. The head is large, equaling the thoracic segments in width, and is produced anterioventrally

into a conical "proboscis." There are three pairs of sclerotized "nodules" ventrally and one pair dorsally, which presumably are sensory organs. The mandibles are long and slender. There are 13 body segments, of which the first 12 diminish gradually in length and width caudad. The last abdominal segment is broad at its base, tapers sharply, and terminates in a cylindrical, ventrally directed tail. This last segment is equal in length to the 9 abdominal segments preceding it. The anal opening is large, situated dorsally at the base of the last segment, and encircled by a sclerotized ring. The head, and the body segments except the last, are heavily sclerotized, and each of the body segments telescopes into the one preceding it.

None of the first-instar larvae of the family that has been studied possesses any indication of a tracheal system, and respiration is consequently by diffusion only.

Second-instar Larvae.—The second-instar larvae of the family reveal differences that are almost as great as those in the first instar. In *Ibalia*, the paired ventral processes have disappeared, and the tail is somewhat reduced. The second-instar larva of *Cothonaspis rapae* retains the eucoiliform characters of the first instar, but the segmentation is more distinct, whereas in *Kleidotoma marshalli* there is a change to the polypodeiform. The head of the latter is very large, exceeding the body segments in width and length, and the segmentation is exceptionally distinct. The minute paired processes occur ventrally on the first 10 body segments. The larva of *Figites anthomyiarum* (Fig. 128*C*) is similar to *Kleidotoma* in all essential respects, though the head is small, the segmentation indistinct, and the tail situated ventrally and at right angles to the axis of the body. An internal tracheal system is present, but there are no spiracles. The second-instar larva of *Charips* sp. (Fig. 126*C*) is still of the caudate form, though the heavy sclerotization of the integument is lacking. Each of the thoracic segments bears a pair of small processes ventrally, and a pair of large conical structures is present at the posterior ventral margin of the head.

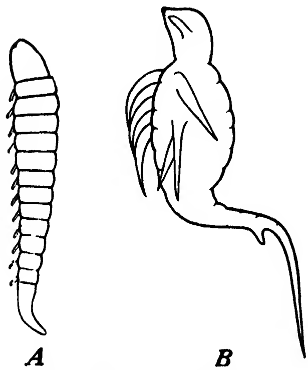


FIG. 127.—*A*, the first-instar larva of *Ibalia leucospoides* Hoch. (*from Chrystal*, 1930); *B*, first-instar larva of *Eucoila keilini* Kieff. (*from Keilin and Baume-Pluvinel*, 1913).

James studied the early instars of cynipoid larvae and came to the conclusion that the eucoiliform first-instar larvae of *Eucoila* and *Cothonaspis* are derived from eggs which hatch in the middle of the protopod stage of embryonic development, whereas the polypodeiform larvae correspond, as the name implies, to the polypod phase. The form of the *Figites* larva, with its reduced appendages and distinct segmentation, indicates hatching in a later embryonic stage than does any of the other species discussed. The *Charips* larva, being devoid of appendages, is regarded as preceding or as being a very early form of the protopod stage. This view of the stage of development at the time of hatching is borne out by the occurrence of polypodeiform second-instar larvae following the eucoiliform first instar in *Figites* and *Kleidotoma*.

Only three instars have been distinguished in the species studied, with the exception of *Ibalia leucospoides*, which has four. The third-instar larva of *Ibalia* is cylindrical in form with the tail still further reduced and may be readily recognized by the presence of spiracles on the second and third thoracic segments.

Mature Larvae.—The mature larvae of the various species differ in only relatively minor characters. That of *Ibalia* has the integument smooth and shining except in the pleural areas of the second to eleventh body segments, which bear rounded

"bosses" studded with minute spines. The mandibles are tridentate, whereas they are bidentate in *Figites* and *Charips*. There is a somewhat surprising variation in the number and position of the spiracles. *Ibalia* has 10 pairs, situated on the second and third thoracic and the first eight abdominal segments; *Eucoila keilini* and *Figites anthomyiarum* have nine pairs, on the last two thoracic and the first seven abdominal segments; *Cothonaspis rapae* eight pairs, on the third thoracic and the first seven abdominal segments; and *Charips* sp. has only six pairs, on the second and third thoracic and the first, second, fourth, and sixth abdominal segments.

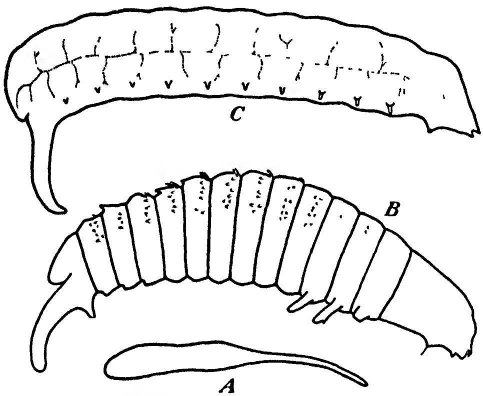


FIG. 128.—Immature stages of *Figites anthomyiarum* Bouché. *A*, the egg; *B*, the first-instar larva; *C*, the second-instar larva. (*From James*, 1928.)

VESPOIDEA

This superfamily is composed of a group of families of exceedingly varied habits and forms. The adults of several families, particularly the Scoliidae, Psammocharidae, and Vespidae, are of large size and striking coloration and are strong fliers, whereas others, particularly the Dryinidae, are small and relatively inconspicuous.

In a considerable number of the families, there is a distinct tendency toward sexual dimorphism among the adults, consisting most frequently in an apterous condition in the females and a much greater size in the males. The alate males of the Thynnidae, Methocidae, and Mutillidae are consistently of appreciably greater size than the apterous females. Among the Bethylidae, the majority of species have alate males and apterous females, though there is not the marked disparity in size that characterizes the above-mentioned families. In some species, subapterous as well as apterous females occur, and in others both apterous and alate forms may be found in both sexes. Apterous females are found in many species of Dryinidae, and the females of the Dryininae are distinguished by remarkable chelate tarsi on the front legs. The complex polymorphism of the Formicidae has been discussed in detail by various authors and need not be dealt with here.

The Vespoidea are, with few exceptions, entomophagous in habit and show a very wide range in host preferences, though the individual families are remarkably consistent in this respect. Among the more important families, the Psammocharidae are predominantly enemies of spiders, the Chrysididae, with very few exceptions, attack the larvae of other vespoid and sphecoid Hymenoptera, and the Thynnidae, Tiphiidae, and Scoliidae are the most important of the parasites of scarabaeid larvae. The Methocidae confine their attack to the larvae of the Cicindelidae, the Bethylidae to lepidopterous and coleopterous larvae, and the Dryinidae to the nymphs and adults of certain families of Homoptera.

There is considerable question as to whether this superfamily should be considered as beneficial or injurious. The evidence at present available appears to favor the beneficial role, particularly in view of the importance of various species of Scoliidae, Tiphiidae, and Dryinidae in the natural control of various crop pests. The Formicidae, which is the dominant family of the order, are usually classed as pests; but in reality their value in the control of many important agricultural pests probably vastly exceeds the damage done.

The host relationships of the entomophagous groups of the superfamily are exceptionally uniform. The parasitic species are external parasites of the immature stages of their hosts, and the great majority are solitary in habit. The Dryinidae are distinctive in that the egg and first larval stages represent a period of internal parasitism. The Bethylidae is the only family having species that are normally gregarious.

The social life of the Formicidae is most complex and has been exhaustively studied by many workers. That of the Vespidae is, of course, much more simple. Even among the parasitic groups there is revealed at times a tendency toward community life. Females of certain species of Bethylidae have been found to live together and rear their broods upon the same host individual; and maternal care of the developing brood is continued, in some species, to the end of the larval period. Several species of Eumenidae depart from the normal habit of the family; instead of provisioning the nest, depositing the egg, and then sealing the cell, the female feeds the larva directly throughout its period of development with chewed-up bits from freshly killed caterpillars.

PSAMMOCHARIDAE

The members of the family are often of large size and present an exceptional uniformity in general characters. The great majority of species provision their nests or cells with spiders, though a few are known to attack beetles, cockroaches, and crickets. Some species attack the host in its own cell or burrow and do not move it after stinging and oviposition have been accomplished. Even the largest spiders are

attacked; the well-known tarantula hawk, *Pepsis formosa* Say, of North America, is an example of the capacity of this group to overcome powerful and active hosts. Williams (1919, '28) has published accounts of the biology and habits of a number of species occurring in the Philippine Islands and South America. A number of genera excavate burrows of considerable length in the soil, or they may utilize natural crevices. Others build clusters of clay or mud cells in sheltered places, such as hollow stems. Each cell is provisioned with a single permanently paralyzed spider, and in some species the legs are amputated prior to transportation to the nest. Ferton (1923) records the habits of a considerable number of species.

A brief account may be given of Williams's observations (1928) on the habits of *Planiceps hirsutus* Banks, which preys upon one of the trap-door spiders in California. The female searches about over the sand dunes until a spider tube is located, whereupon she digs down into the

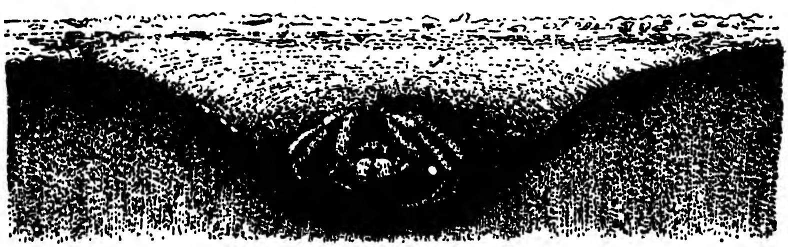


FIG. 129.—A vertical section through the funnel nest of *Pompilus analis* F., showing a female ovipositing upon *Heteropoda gemella*. (*From Williams*, 1919.)

sand a short distance away, apparently with the object of causing sufficient disturbance to drive the spider out of the tube. This act may be performed several times, and eventually the trap door flies open and the spider rushes away. It is quickly overtaken, however, and stung into insensibility. The *Planiceps* female then grasps it by a leg and drags it into the tube that it had abandoned a few moments before. The trap door is pulled shut and apparently fastened, after which the egg is deposited upon the abdomen of the victim.

Most species prepare their own nests for reception of the prey. Various means are employed in transporting the victims to the nest. One of the most interesting is that of *Priocnemis* and others of dragging the prey over water. The female is apparently unable to carry such a heavy burden in sustained flight, but the buoyancy of the spider body permits the wasp to skim along the water surface with it (Rau, 1934).

We are more particularly concerned with the specialized habits of the strictly parasitic members of the family rather than with those which provision their nests. Iwata (1932) has recently published an extended

account of *Homonotus iwatai* Yasum., which parasitizes the adult females of the spider, *Cheiracanthium rufulum* Kishida, in Japan. This spider has the habit of folding a leaf of one of the larger grasses in a characteristic manner, to form an oviposition chamber. The leaf is bent upon itself twice, and the adjacent margins are fastened together with silk; thus a three-sided chamber is formed, 2 to 4 cm. in length.

The *Homonotus* females appear in the field during July, at which time the spider hosts have formed their oviposition cells and either have not yet begun oviposition or have deposited only a few eggs. The parasite enters the cell either by prying apart the lightly joined leaf margins or by cutting a hole directly through the leaf. The spider is stung very quickly and the egg deposited dorsally and transversely at the base of the abdomen. Paralysis is complete but not permanent, and in about 30 minutes the spider is moving about, though rather sluggish. In laboratory experiments, feeding took place when suitable food was provided. The most noticeable effect of the sting is in the complete prevention of oviposition by the host. Hatching of the parasite egg takes place two or three days after oviposition, and larval feeding is complete in five days. The cocoon is spun within the cell of the host. Nielsen (1936) records similar habits for *H. sanguinolentus* F. in Europe, except that the host is permanently paralyzed.

The wasps of the genus *Notocyphus* temporarily paralyze their hosts, which are principally aviculariid spiders, in the open and deposit the egg dorsally at the base of the abdomen. The host's activity is greatly reduced after this attack; feeding is limited, or it may be entirely discontinued.

A number of species in the family have abandoned the habit of capturing living spiders themselves; instead, they consistently make use of those which have already been captured by females of other species. *Xanthampulex luzonensis* Roh. (Williams, 1919*b*) has the habit of depositing its egg upon that of *Pompilus analis* F.; because of its shorter incubation period, this egg hatches first, and the young larva destroys the egg of the latter and completes its development upon the spider provided by the *Pompilus* female. This is somewhat similar to the habit of several species of *Ceropales*, one of which was noted by G. Adlerz to deposit her egg in a breathing pore of the spider's abdomen during the time it is being dragged to the nest by a *Pompilus* female. The *Ceropales* egg hatches first, and the larva then destroys the egg or young larva of *Pompilus* and completes its development upon the spider. Ferton gives an account of *P. pectinipes* Lind., which has the extraordinary habit of digging down into the soil to the cells of other species of the genus, removing the eggs of the latter from the spider prey, and substituting her own.

The cocoons of the species that develop in cells in the soil often have a marked resemblance to those of the Scoliidae and Tiphiidae. The pupa of the Psammocharidae, however, can be readily distinguished from those of the above families by the presence of highly developed lateral processes upon the abdomen, which serve as braces to hold it away from direct contact with the cocoon wall.

CLEPTIDAE

The family is represented by the single genus *Cleptes*, which is found in Europe, North America and Asia. The habits, aside from the host

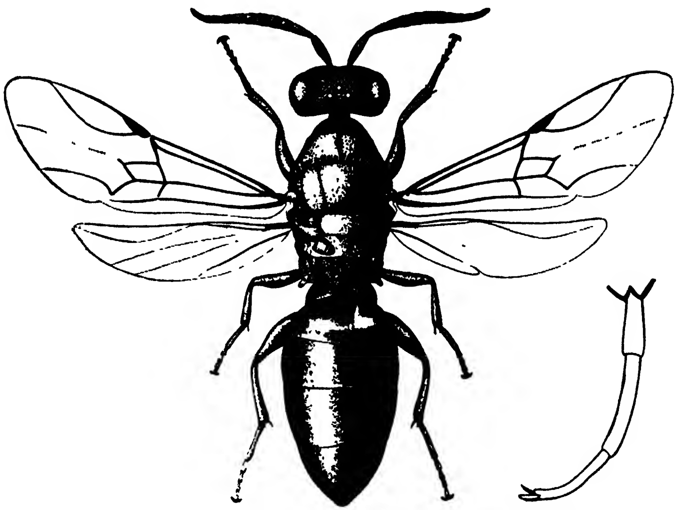


FIG. 130.—The adult female of *Cleptes* sp., with the extruded ovipositor at the right.

preferences, are unknown except for an undetermined species observed in Chosen (Korea), which is a solitary external parasite of the prepupae of various sawflies in the cocoon. In general appearance and habit, this species has a striking resemblance to the parasitic Chrysididae. Several other species have been reared from sawfly cocoons in various parts of the world.

The adult female of *Cleptes* sp. (Fig. 130) is extremely active and spends the greater portion of her time upon the ground in search for sawfly cocoons. When one is found, she gnaws a hole in the cocoon wall, and through this opening the extensible ovipositor is inserted by a backward thrust. When extended the ovipositor is longer than the abdomen and is three-jointed. The egg is placed horizontally upon the host body in the mid-ventral curve of the abdomen but does not adhere thereto. When oviposition is complete, the female smears a quantity of mucilaginous material over the hole in the cocoon wall and thus seals it

effectively. Parasitized cocoons can be readily recognized by this spot of hard, glistening material. This oviposition habit is identical, in its essential respects, with that of *Chrysis shanghaiensis* Smith, which attacks certain lepidopterous cocoons.

The egg (Fig. 131*A*) is subelliptical in form with the anterior end widest, is 1.0 mm. in length, and bears a button-like micropylar structure.

The first-instar larva (Fig. 131*B*) has 12 indistinct body segments of equal length, and the caudal end tapers to a rounded point. The head is large, quadrangular in outline, and not heavily sclerotized and bears conspicuous antennae at the dorsal anterior corners. The mouth is situated ventrally, and the mandibles are small and simple. There are no integumentary spines or setae. Eight pairs of spiracles are present, situated at the anterior margin of the first thoracic and on the first seven

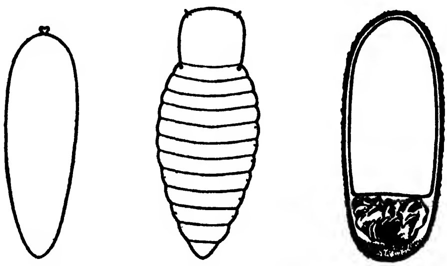


FIG. 131.—Immature stages of *Cleptes* sp. *A*, the egg; *B*, the first-instar larva; *C*, the cocoon of the sawfly host, showing the *Cleptes* cocoon within it and partitioning off the host remains.

abdominal segments. The first pair is exceptionally large, whereas those on the abdomen are small and inconspicuous.

The mature larva is very robust, glistening white in color, and bears 10 pairs of spiracles. A distinct parchment-like cocoon (Fig. 131*C*) is spun within that of the host, and its posterior end is flattened to partition off the host remains and meconium, which are compressed into a mass.

Incubation of the egg requires 4 days, and the larval period is complete in 10 days. The host prepupa is consequently killed without attaining the pupal stage. The total cycle from egg to adult is approximately five weeks, and there are several generations each year.

CHRYSIDIDAE

The Chrysididae are large insects of brilliant metallic coloration, usually green or blue, with coarse sculpturing, and are variously known as cuckoo wasps, ruby wasps, and gold wasps. They are predominantly solitary external parasites of vespoid and sphecoid Hymenoptera, though a few are inquilines in the nests. The great majority attack hosts that form their nests or cells in exposed places, such as the mud cells

upon walls, in crevices, etc., or those in hollow plant stems. Certain species, however, are known to confine themselves to hosts that burrow in the soil. *Chrysis shanghaiensis* Smith is the single representative of the family known to be parasitic upon lepidopterous larvae. As a whole, the family must probably be considered more injurious than beneficial because of attack upon hosts that store their nests with injurious insects and upon hosts that are beneficial because of their habit of gathering pollen or nectar, which results in blossom pollination. Very few species are sufficiently abundant, however, to be of economic importance.

The adults of the hymenopterous hosts of the Chrysididae are often efficient fighters, and this presumably has been responsible for the development of defensive measures by the parasite identical with those employed by many other animals having a heavy carapace. The females, when disturbed or attacked, often roll themselves into a compact ball (Fig. 133) and remain immobile in that position, thus effectively shielding the vulnerable points of the body from injury.

BIOLOGY AND HABITS

C. shanghaiensis, which occurs throughout Asia, is perhaps the most interesting of the strictly parasitic members of the family, and detailed accounts of its habits have been published by Piel (1933*a*) and D. E. Parker (1936). It is a solitary external parasite of the mature larva of the oriental moth, *Monema flavescens* Wlk., within its hard, egg-like cocoon, in southern Japan and China. This cocoon is much too hard to be penetrated by the female's flexible ovipositor; instead, she bites away a small hole with her mandibles. During the process, she slowly rotates the body about the point of attack, and the surface markings at the point of penetration are consequently in the form of radiating lines. When the hole is of sufficient size, she turns about, inserts the ovipositor, and stings the host larva in the thoracic region, effecting permanent paralysis. It is believed that this stinging is for the purpose of preventing transformation to the pupal stage, rather than merely to immobilize the host. The egg is then laid loosely upon the body. Following the deposition of the egg, the female again applies her mandibles to the orifice, scraping from the surface of the cocoon material that, with the pellets set aside at the time the opening was made, is mixed with an oral secretion and used as a plug to seal the aperture. Parasitized cocoons can be readily recognized by the radiating lines surrounding the point of penetration, which extend outward 1 or 2 mm. The time elapsing from the beginning of penetration of the cocoon to the final sealing of the puncture averages approximately one hour.

The first-instar larva is active, and, while feeding, it uses the bifurcate caudal process as a brace against the cocoon wall. The mature larva

spins a silken, golden-colored cocoon within that of the host, and the meconium is discharged through the strands of the partly formed cocoon into the posterior region of the host cocoon, which contains the remains of the *Monema* larva. Emergence is always from the anterior end of the host cocoon.

The cycle from egg to adult is completed in about six weeks, of which 2 to 4 days is required for incubation of the egg and a minimum of 11 days for the pupal stage. The larval feeding period is followed by a rest period of approximately equal length. In the first generation in south China, the total duration of the cocoon stage is approximately 21 to 25

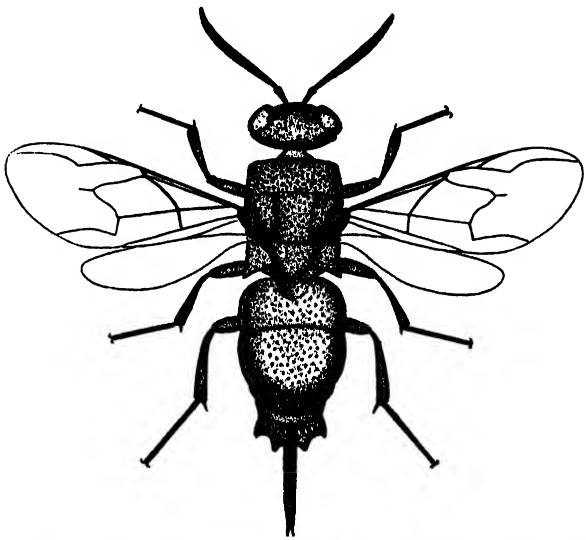


FIG. 132.—The adult female of *Chrysis coerulans* F. (*Redrawn, after Cameron,* 1888.)

days. The adults are long-lived, and the females may persist in the field for several months. The reproductive capacity is low; an average of only 11.3 eggs per female was secured by Parker under experimental conditions. In China, the field parasitization approximates 50 per cent.

Two generations are produced each year in south China, corresponding to the cycle of the host, but only a single brood developed under experimental conditions in Massachusetts. Hibernation is in the mature larval stage.

The species of Chrysididae that are parasitic upon Hymenoptera usually attack the host in the mature larval or prepupal stage and are not dependent at any time upon the provisions contained in the host cells. *C. pacifica* Say (Hicks, 1933) apparently oviposits at any stage of development of the larva of its host, *Alcidamea brachyodonta* Ckll., but the first-instar larva delays its attack until the host cocoon is spun and the

prepupal stage attained. *Pleurocera viridis* Guer. and *Tetrachrysis carinata* Guer. (Janvier, 1933) oviposit through the cement-like cell wall of the *Odynerus* cell and only after the cocoon of the latter has been formed. Penetration of the cell wall requires a period of one to three hours, and this is accomplished by use of the ovipositor alone. *C. viridula* L. (Chapman, 1869) which attacks *Odynerus*, also, usually chooses the less protected cells for oviposition and may lay its eggs in those which, for any reason, are still open. In the case of closed cells, there is some indication that the mandibles are used in making the perforation. Six to ten eggs are placed upon each host, but the surplus is destroyed by the larva that hatches first.

The habits of *C. lusca* var. *concinna* Grib. (Bordage, 1913) differ markedly from the species already discussed. The egg is deposited shortly after that of the host, *Sceliphron*, and the first-instar larvae of parasite and host engage in combat, after which the survivor develops upon the prey contained in the cell. If the host egg fails to hatch, the *Chrysis* larva dies without touching the food supply. This indicates that *Chrysis* is an obligate predator upon the first-instar larva of *Sceliphron*, and after this host has been consumed its food requirements are met by the spiders with which the cell is stocked. In the case of *Chrysis dichroa* Dhlb. (Ferton, 1923), which develops in the cells of *O. rufohirta* Latr. in Europe, the egg is laid in the cell before the latter is closed and on the food material at the opposite side from that occupied by the *Osmia* egg. Hatching takes place slightly before that of the host. Though a number of eggs may be deposited in a cell, yet only one larva survives beyond the first instar. Normally the parasite does not attack the *Osmia* until larval development is complete, though occasionally the egg may be destroyed. Similar habits are recorded for *C. prodita*, which is parasitic upon *O. saundersii* Vach.

FIG. 133.—A female of *Chrysis parvula* F. in the characteristic rolled-up position assumed when attacked. (*Photograph by Bureau of Entomology and Plant Quarantine.*)

Pseudochrysis neglecta Shuck. (Maneval, 1932) is the only species of the family known to develop as an internal parasite. The first-instar larva penetrates the body of the partly grown larva of *Osmia villosa* Schnck. and develops coincidentally with it. The internal feeding period covers about 20 days, and the body contents of the host are entirely consumed.

All species spin a cocoon within the host cell, and in the majority of cases it is within the host cocoon, also. *C. viridula* first forms a mirror-like diaphragm across the center of the host cocoon, separating off the

host remains, and in this chamber the parasite cocoon is spun. This separation of the host remains from the cocoon by a partition appears to be general in the family.

The developmental period of most species, from hatching to the completion of feeding, is relatively short. Incubation of the egg requires 2 to 5 days, and the larval feeding period ranges up to 30 days. The minimum is recorded for *C. ignita*, which completes feeding within 6 days after oviposition. In the summer broods, a resting period of some length intervenes before pupation. A number of species have a single generation each year; whether or not there is more than one is probably correlated with the cycles of the hosts themselves. Hibernation takes place in the mature larval stage in the cocoon. The period of occurrence of adult Chrysididae in the field is often considerably shorter than that covered by the nesting activities of the hosts, and a portion of the host brood is consequently exempt from attack.

A curious mating habit is described by Janvier in the case of *T. carinata* in Chile. The male, which emerges earlier than the female, is apparently able to detect the presence of the latter while she is still within the cell of the host. When a cell containing a female is encountered, the male attacks the cell wall with the mandibles, eventually making a passageway into the interior, and then tears open the cocoon. The female is seized by the thorax and dragged out of the cell, and mating is then accomplished.

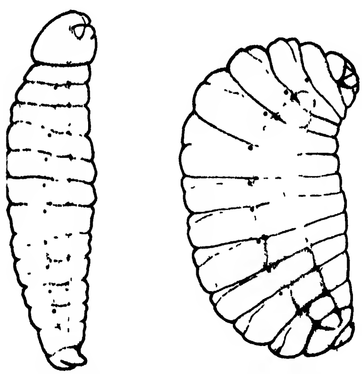


Fig. 134.—The first (at left) and last instar larvae of *Chrysis shanghaiensis* Smith. (*From D. E. Parker*, 1936.)

IMMATURE STAGES

The eggs of only a few species of the family have been described. That of *C. shanghaiensis* is 2.1 to 2.5 mm. in length, about one-fifth as wide, cylindrical, and slightly curved. There is a minute protuberance at the anterior end, and the chorion is finely roughened. In other species, the anterior end is slightly wider, and no protuberance at that end has been mentioned in the descriptions.

Five larval instars have been detected in the few species upon which close observations of larval development have been made. The first-instar larva of *C. shanghaiensis*, (Fig. 134), which is quite typical of the family, has 13 distinct body segments, with a relatively large, quadrangular head and simple mandibles. The caudal segment of the body is bifurcate. Integumentary spines and setae are lacking. The nine pairs of spiracles are situated on the second thoracic and first eight abdominal segments. In *C. pacifica* and *C. dichroa*, each body segment bears a ring of rather heavy spines. The caudal segment of *Pseudochrysis neglecta*, as described by Maneval, is more highly developed than in other species; and each lobe bears three rings of setae, and the tip is heavily sclerotized. Ventrally and dorsally at the base of each

lobe is a fleshy spine or protuberance. The two lobes are curved inward and can be employed, forceps-like, for locomotion and combat.

The intermediate-instar larvae are similar in form and may be distinguished from the first by the more robust body, the absence or great reduction of the bifurcate caudal process after the first molt, the greater number of spiracles, and the dentate mandibles. In *C. shanghaiensis*, the tenth pair of spiracles, on the metathorax, appears on the second-instar larva, and their number and arrangement then persist unchanged until maturity. The mandibles are tridentate in the second to fifth instars. These characters of the mature larva appear to be uniform for the family.

SAPYGIDAE

The family comprises relatively few genera and species, of which the habits are little known. They are said to be either parasites or inquilines in the nests of various Sphecoidea and Apoidea. H. L. Parker (1926) has studied the habits of *Polochrum repandum* Spin. in Europe, which develops in the cells of *Xylocopa violacea* L. The young larva is found on the food mass in the cell with the egg of *Xylocopa*, and the latter is apparently destroyed before extended feeding takes place on the stored food.

THYNNIDAE

This group of wasps is of particular interest because of the marked difference in size between the males and the females, the apterous condition of the latter sex, and the mating flights that occur in practically all species. The members of the family are found commonly only in Australia and South America. The host preferences are definitely known for only a comparatively few species, but these indicate that the insects attacked are primarily the grubs of Scarabaeidae in the soil or in decaying wood. It has been suggested that many species may be parasitic on other aculeate Hymenoptera, but this has not been substantiated by rearings from such hosts. The Australian *Diammia bicolor* Westw., which is questionably assigned to this family, is parasitic upon the mole cricket, *Gryllotalpa coarctata* Wlk. The most comprehensive studies on the biology and habits of the Thynnidae are those by Janvier (1933) on a series of species, principally of the genus *Elaphroptera*, occurring in Chile, and by Burrell (1935) on some Australian species.

Elaphroptera dimidiata Guer. is representative of the series of species studied by Janvier in Chile. It is a solitary external parasite of the grubs of the scarabaeid genera *Oryctomorphus*, *Amblyterus*, and *Liogenys*. The adult males become active in the field shortly after sunrise and may be seen in numbers circling just above the surface of the ground. They center about certain points that prove to be those at which females are about to emerge. The female is dragged from her burrow and the mating flight begins, which may cover a period of one hour or more. These mating flights may occur frequently during the life of the female.

The females pass the night singly under rubbish on the surface of the ground, and at dawn they ascend the trunks of trees, where they take up the characteristic inverted waiting position. It has been established that the females exercise an attraction for the males only when in this position and not when they are moving about, the stimulus being visual rather than olfactory. The males cluster together at night in galleries in the soil or upon the foliage of plants.

The males feed extensively at blossoms and upon sap exuding from wounds in tree trunks caused by boring beetles. The females also feed upon plant sap but not at blossoms, and their principal food is the body fluids of host grubs.

In practically all species of Thynnidae, the males carry the diminutive wingless females about for an hour or more in the mating flight. *D.*

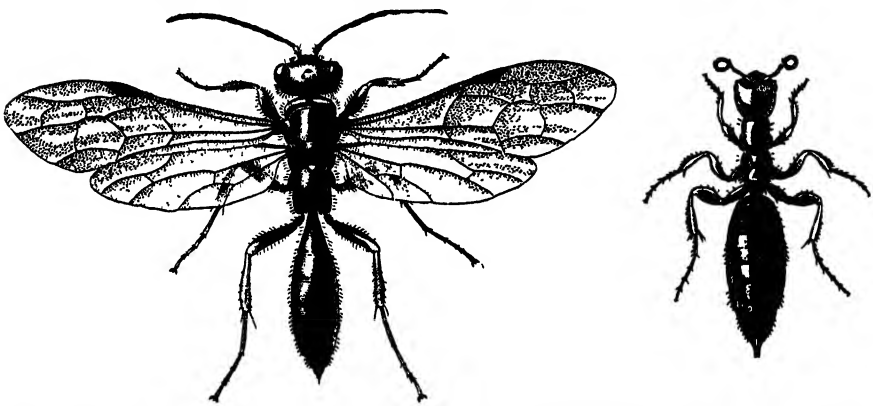


FIG. 135.—The winged male and apterous female of *Neozeleboria proximus* Turn. (*From Burrell*, 1935.)

bicolor (Turner, 1907), however, does not have this habit, and the male is smaller than the female. Burrell's observations indicate that the females, and not the males, feed extensively at blossoms during this flight period, which is contrary to earlier reports. The mating flight serves two purposes in addition to its primary object, these being the securing of food for the female and the dissemination of the species. Manifestly, the dispersion would be exceedingly slow if dependent entirely upon the locomotory capacity of the apterous females.

In oviposition, the host grub is first permanently paralyzed and the egg then placed longitudinally at the lateral margin of the thorax opposite the last pair of legs (Fig. 136). The egg is somewhat cylindrical, is curved, with one end slightly broader than the other, and is stated to be attached to the integument by a short filament. Hatching takes place 10 days after deposition, and the entire body of the host, with the exception of the head and the integument of the anterior portion, is

consumed by the larva. Feeding is complete in 15 days, after which there is a resting period of about one week and the cocoon is then spun. A single generation is produced each year, and the winter is passed in the adult stage in the cocoon in the soil.

Feeding by the females of the Chilean *Elaphroptera* upon the body fluids of the host is very extensive. The grubs used by *E. atra* Guer. for feeding purposes are not stung, and the female merely chews the posterior portions of the body. Such individuals invariably die. About 50 per cent of field-collected grubs of *Athlia rustica* Er. showed these feeding

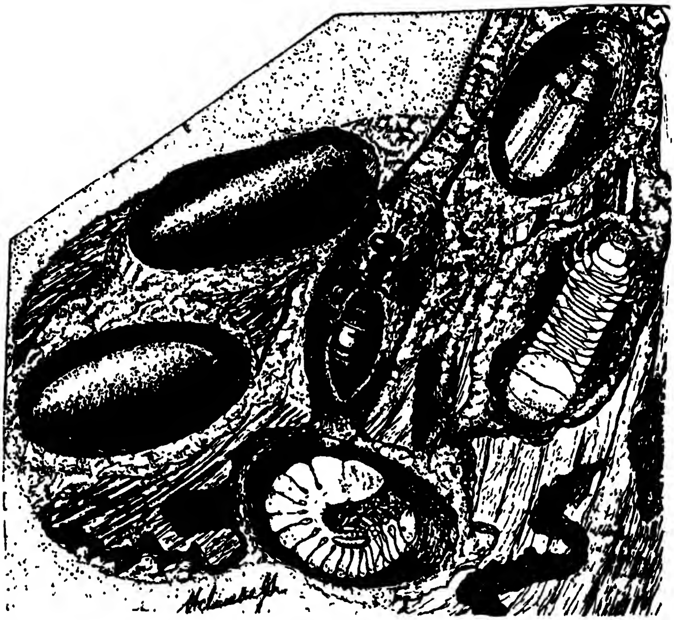


FIG. 136.—A female of *Elaphroptera dimidiata* Guer. in a burrow in decaying wood, with a host grub bearing an egg (below) and two cocoons in the host cells (at left). (*From Janvier*, 1933.)

wounds produced by *E. herbsti* André, and the species may consequently be of greater value as a predator than in its parasitic role. Burrell, however, does not mention this habit in the Australian species.

All the Thynnidae, with the exception of *Diamma*, attack the host grub in its cell and do not move it. These hosts, except for those attacked by *Diamma*, are permanently paralyzed. *D. bicolor* stings the host and drags it to a previously prepared burrow, in which it recovers its power of movement in about one hour.

The position preferred for oviposition by several species of Chilean *Elaphroptera* is at the side of the thorax, the egg lying parallel with the body axis of the host. Burrell, however, found that the Australian

species which he had the opportunity to observe, representing five genera, all place the egg on or near the median ventral line of the second to fourth abdominal segments. The same is true of *Epactiothynnus opaciventris* Turn., observed by Williams (1919*d*) in Australia. The anterior end of the egg lies toward the head of the host.

The life cycles of the majority of species probably cover one year, to conform to the cycles of the host. The egg of *Elaphroptera dimidiata* requires 10 days for incubation, whereas those of the Australian species hatch in two or three days, and the larval feeding period in general is short, ranging from 5 to 10 days. The longer developmental period noted by Janvier is very probably correlated with the much lower temperatures prevailing at the elevations at which the South American species were found.

Very little information is available regarding the characters of the immature stages. The eggs which have been described are rather elongate, have the anterior end slightly broader, and are somewhat curved. No details are available regarding the "filament" that is stated by Janvier to attach the eggs of several species of *Elaphroptera* to the host integument.

The feeding habits of thynnid larvae are comparable with those of *Campsomeris* and *Scolia*, in that a large hole is torn in the skin of the host and the head is embedded therein. This hole is so large that there is often a considerable exudation of fluids from around the head. The newly hatched larva, however, is capable of considerable movement, and its point of feeding is consequently not determined by the position of the egg.

The larvae of the family are readily distinguished from those of the Scoliidae and Tiphiidae by the very faint segmentation of the body as compared with a pronounced segmentation in the latter groups. In several species of *Elaphroptera* described and figured by Janvier, the mandibles of the mature larvae are tridentate, and the spiracles occur only on the first nine abdominal segments. This spiracular arrangement is not found elsewhere in the order; but if it proves to be general for the family, it will serve as a ready means of distinguishing the larvae from those of the above two families, which have the same host preferences.

The cocoons are somewhat similar to those of the Scoliidae, and the posterior end is not so pointed as in the Tiphiidae. The cocoon wall is composed of many closely appressed layers of silk, and a varying quantity of loosely woven strands may fill the space between the cocoon and the cell wall. At emergence, a circular cap is cut away at the anterior end.

TIPHIIDAE

The family Tiphiidae is the dominant group of hymenopterous parasites attacking scarabaeid grubs in the soil. All species are solitary and

develop as external parasites, usually upon the final larval instar of the host. The genus *Tiphia* is cosmopolitan and by far the most common of the family. A general study of a considerable number of species has been given by Clausen *et al.* (1932). *Myzine* is also a well-known genus with similar habits, whereas *Pterombus* departs from the otherwise consistent host preferences of the family by attacking the larvae of Cicindelidae.

A considerable number of species have been utilized in the attempted biological control of scarabaeid pests, the more extensive efforts being against *Phytalus smithi* Arrow in Mauritius and *Popillia japonica* Newm. in the United States. It cannot be said that the species introduced have had any pronounced effect thus far in reducing the pest population. Practically all members of the family are limited by the food supply of the adults, and the bulk of oviposition normally takes place within a very short distance of the feeding grounds. For this reason, large concentrations may be found in certain places, not necessarily in the areas of heavy grub infestation, and relatively few adults may reach these areas after feeding. A high parasitization may be attained in small areas, but the general average is usually low.

BIOLOGY AND HABITS

Habits of the Adult.—The food of the adult Tiphiidae varies with the season, but the spring species almost invariably subsist upon the honeydew secretions of aphids, scale insects, leaf hoppers, and other bugs. During the late summer and autumn months, however, this source of food is largely lacking, and the species that occur at that time feed instead at blossoms of various plants, particularly the Umbelliferae, and at the nectar glands of *Polygonum*, sweet potato, etc. A two-generation species will consequently feed upon honeydew in the spring and mainly upon plant exudations in the second generation. The species of *Myzine* are chiefly blossom feeders throughout the season. The wasps are evidently attracted to their food by odor, for at a colony site surrounded by feeding areas they are found feeding only on the windward side. The most striking illustration of this habit is shown by *Tiphia matura* A. & J. in India (Clausen *et al.*, 1933), which travels several miles and to a considerable elevation to the aphid-infested plants at which it feeds and then returns for oviposition. Adult feeding usually covers a period of about two hours during the morning, and the males appear slightly earlier, and likewise disappear earlier, than the females. On bright days, *T. popilliavora* Roh. consistently feeds from 10:00 A.M. until noon, whereas other species may be somewhat earlier, as was found in *T. matura*, which appears at 8:00 A.M. and may remain until 11:00 A.M. Mating generally takes place upon the foliage during the course of feeding.

Another source of food is the body fluids of the grubs attacked by the female wasps. This habit has been observed only in *T. popilliavora,* in which species the female, after deposition of the egg, may bite or chew one of the legs of the grub until a puncture is made or the leg entirely bitten off, after which she imbibes the fluids that exude from the wound.

In attack upon the host the female *Tiphia* burrows into the soil and gains access to the cell occupied by the grub. As observed in the case of *T. popilliavora,* she first crawls over the dorsum of the body from the rear, then curls the abdomen down and around the side, and inserts the sting in the venter of the thorax, usually between the first two segments. This stinging is repeated until the grub is quiescent. She then turns to the abdomen and commences an extensive kneading of the ventral surface with the mandibles, beginning with the first segment and

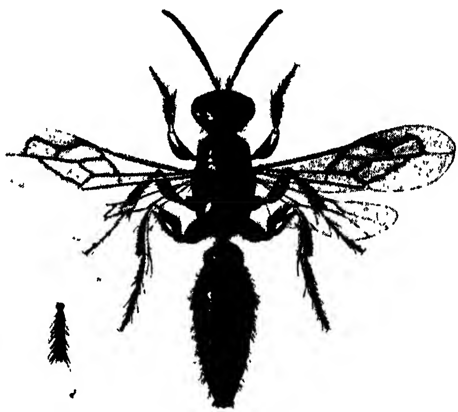


FIG. 137.—The adult female of *Tiphia popilliavora* Roh. (*From Clausen et al.*, 1927.)

continuing for its entire length. When this is complete, she grasps the lateral margin with the mandibles and coils the body transversely over the dorsum and to the ventral surface, forming almost a complete circle. The tip of the abdomen is applied to the groove between the fifth and sixth abdominal segments, near the margin, and is rhythmically moved backward and forward for several minutes, thus broadening the groove and possibly rasping away a portion of the integument to permit of more ready penetration by the larva. In the course of this preparation, any egg or young larva that may be present as a result of an earlier oviposition is rubbed off or broken. The egg is finally extruded and is firmly attached by a mucilaginous material. It lies transversely in the groove, with the anterior pole directed toward the median ventral line of the host body. The wasp may then quit the body or remain for a period of feeding, as has already been described. The grub recovers from the effects of the sting in 20 to 40 minutes.

The manner of attack by the females of other species upon the host grubs is relatively uniform and corresponds to that described for *T. popilliavora*. The kneading of the body does not occur in all species, being omitted entirely by those which oviposit dorsally, and is much restricted in the species which place the egg ventrally on the anterior portion of the body. Usually any egg or young larva already present on the host is rubbed off or destroyed before the fresh one is laid. An exception to this rule is *T. bicarinata* Cam., which frequently accomplishes duplicate oviposition. No instance is known of female *Tiphia* moving the host grubs after stinging; they are left in the feeding cell in which they were found. In several instances, however, *Myzine* females have

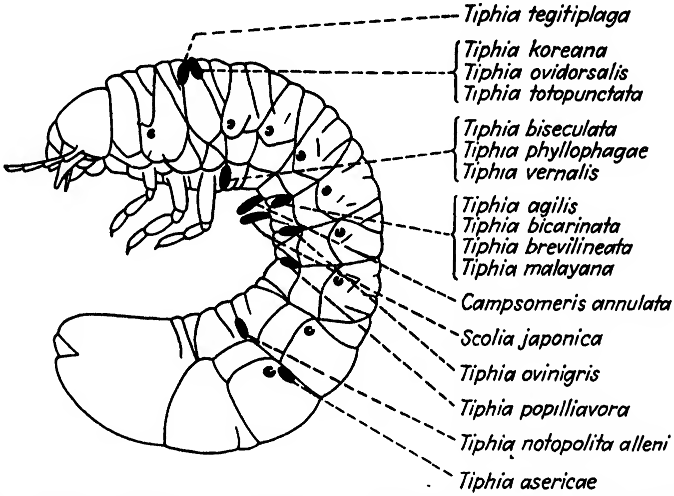


FIG. 138.—The egg positions of a series of Tiphiidae and Scoliidae. (*From Clausen et al.*, 1932.)

been observed to attack grubs on the surface of the ground and to bury them after stinging. All species of *Tiphia* paralyze the host only temporarily, whereas the few species of *Myzine* and *Pterombus* that have been studied effect permanent paralysis.

The great majority of species attacking Scarabaeidae show a decided preference for mature hosts for oviposition, though in case of necessity they will attack grubs that are half-grown or even smaller. This is particularly true of those which parasitize host species having an annual cycle. In contrast to this, a number of species that attack hosts having a two- or three-year cycle, such as many *Phyllophaga* and *Anisoplia*, habitually oviposit upon the second-instar grubs rather than the third.

The oviposition habits of the South American *Pterombus cicindelicidus* Williams and *P. iheringi* Ducke have been observed by Williams (1928). These species are parasitic upon tiger-beetle larvae of the genera *Cicindela*

and *Megacephala*, respectively. The adult wasps are more slender and active than those of *Tiphia*, and the method of attack upon the host brings to mind that of *Methoca*. The female searches about the surface of the ground for open or recently closed tiger-beetle burrows, and, if one is found and proves to be open, she plunges into it and attacks the larva. In case it is closed, she burrows downward until the larval cell is reached. The head of the victim is seized between the mandibles and the abdomen then brought forward and the sting inserted in the throat or thorax, resulting in complete and permanent paralysis. The wasp now attempts to push the inert body near to the entrance to the burrow, and finally the egg is deposited longitudinally and somewhat to one side of the median ventral line of the second or third abdominal segment.

The position in which the egg is placed upon the body of the host grub is virtually constant for any given species (Fig. 138); the variation between species is with respect to the segment upon which the egg is deposited, ventrally, laterally, or dorsally, and the orientation of the egg is with respect to the median line. The majority of species place the egg transversely in a groove between two abdominal segments ventrally, several placing it immediately behind the last pair of legs. Always it is some distance from the median line and usually near the lateral folds. *T. asericae* places the egg dorsolaterally in the groove between the seventh and eighth abdominal segments just above the last spiracle. In the case of other species, it is placed dorsally on the thorax, just to one side of the median line, and most often in a groove on the third segment.

The position of the egg on the host body usually does not vary more than one segment from the normal for the species. Marked deviations from this occur only in case of excessive duplication of oviposition on a grub, for a female will not deposit an egg in a groove that previously bore one. The predominant position may also vary one segment if a different instar or host species is attacked. In the majority of species that deposit the egg ventrally, the anterior pole is directed toward the lateral margin of the host body. This position is governed by the length of the body of the parasite female with respect to the circumference of the body of the host grub. In oviposition, she grasps a lateral fold with the mandibles and curls the body over the dorsum and around to the venter. If a nearly complete circle is described and the ovipositor lies practically beneath the head, the egg that is deposited has its anterior pole directed toward the median ventral line of the grub body. In case it extends only to the opposite side, the pole is directed outward. Davis (1919) states that the egg of *Myzine 5-cincta* F. is placed diagonally on the venter of the sixth or seventh abdominal segment, whereas that of *M.*

ephippium F. (*xanthonotus* Roh.) is placed longitudinally upon the venter of the abdomen (Jepson, 1936). The habit of placing the egg longitudinally, rather than transversely in an intersegmental groove as is done by *Tiphia*, may be general in the Myzininae.

It has been pointed out that the female Tiphiidae, at least of the genus *Tiphia*, oviposit upon the host grub in its cell in the soil and do not attempt to bury it at a greater depth, which is in contrast to the habit of the Scoliidae. As a result, the cocoons of most species are found near the surface, though in the species that attack the host rather late in the autumn the cocoons are often found at as great a depth as those of the Scoliidae. McColloch *et al.* (1928) mention that in Kansas they were found as deep as 60 cm. and that the average depth over a period of years ranged from 25 to 45 cm. This is below the winter frost line. The occurrence of *Tiphia* cocoons at such depths can be explained by the habits of the host grubs. The lateness of the season at which oviposition takes place and the attendant low temperatures extend the time intervening between parasitization and death; and during this period, while the grubs are still active, they follow their natural tendency to descend deep into the soil for hibernation. Here the parasite larvae complete their development and spin their cocoons.

Larval Development.—In *T. popilliavora*, the hatching of the egg is effected by a longitudinal split of the chorion over the head and thorax of the larva. The head is then extruded, and a feeding puncture is made. As the larva becomes larger, the shell splits nearly to the posterior end; it then lies as a pad beneath the body and adhering firmly to it. Each successive instar makes a new feeding puncture a short distance in front of the preceding one. The successive cast skins remain in leaf-like form, adhering to the ventral side of the body. There are thus five feeding punctures, with the mouth parts of the larva embedded in the first four, and the eggshell and four cast skins beneath the body of the last instar. In the latter part of the final stage, suctorial feeding is abandoned, and the entire host body, with the exception of the head and legs, is consumed. Death of the host does not take place until the parasite is in its fifth larval stage.

Larval development in other species of the genus does not differ from that described above. Vassilliev (1914) mentions that the mature larva of *T. femorata* F. enters the empty skin of its host, *Anisoplia austriaca* Hbst., and spins its cocoon therein.

The meconium is cast by the mature larva after spinning of the cocoon is completed and is found in the form of a disk-like pad at the posterior end.

The cocoons of the Tiphiidae are more slender than those of the Scoliidae and of different form, being broader at the anterior end and

smoothly rounded, and tapering to a point at the posterior end. The wall is very dense and compact, with a highly glazed inner surface. Surrounding the cocoon is a mass of silken strands of varying amount, either in the form of a loose, fluffy covering or as a series of thin, distinct envelopes. The cocoon of *T. brevilineata* A. & J. differs from that of other species of the family in lacking almost entirely the outer covering, and the outer cocoon surface is somewhat glazed and uneven. That of *M. ephippium* is stated by Jepson to have an outer covering separable into more than 20 distinct layers of silk. The color of the cocoons ranges from tan to a deep brown, this being due, in part at least, to the composition of the surrounding soil. Those spun free from soil are almost white.

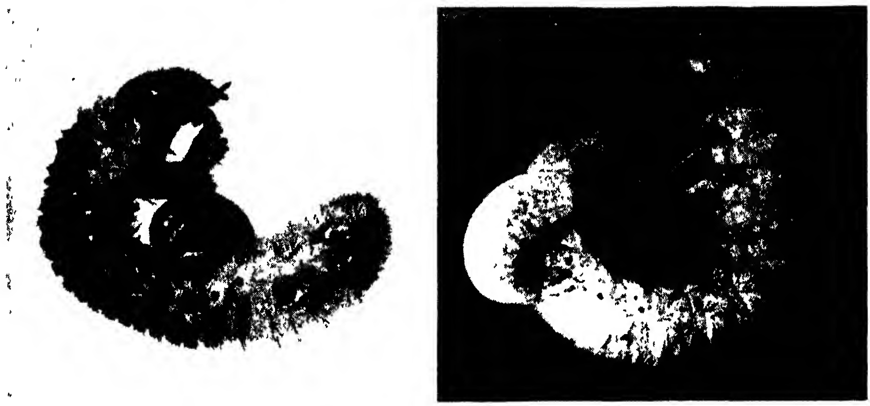


FIG. 139.—Larvae of *Tiphia popilliavora* Roh. (at left) and *T. asericae* A. & J. *in situ* on host grubs. (*Photographs by Bureau of Entomology and Plant Quarantine.*)

The cocoon of *Pterombus* resembles that of *Methoca* in having the outer covering flaring at the anterior end.

Cocoons from which *Tiphia* adults have emerged may be recognized by the form and position of the emergence hole, which is slightly to one side of the anterior end and has an irregular and roughened edge. This is because the adult bites away the cocoon wall and covering bit by bit, whereas in the Scoliidae a large circular cap is cut away, leaving a smooth, even margin. The emergence holes of *Myzine 5-cincta* and *M. haemorrhoidalis* F. are similar to that of *Tiphia*.

Reproduction.—The reproductive capacity of the members of the family is comparable with that of the Scoliidae, with a general average of approximately 50 eggs, deposited during a period of three to four weeks. Many species are able to maintain an oviposition rate of two eggs per day. A marked difference has been noted in the total number of eggs laid by the Chinese strain of *T. popilliavora* as compared with the Japanese strain. Under insectary conditions, a series of the former averaged 54.9

eggs each, with a maximum of 115, as compared with an average of 36 for the latter under identical rearing conditions. D'Emmerez de Charmoy states that the capacity of *T. parallela* Smith is approximately 70 but that the eggs are normally laid by two's, at intervals of six to eight days, and consequently the oviposition period is greatly prolonged as compared with that of species occurring in temperate regions.

In parthenogenetic reproduction, the progeny are, as far as known, exclusively male. The great majority of species studied are capable of reproducing in this way, though Davis states that this is not the case in *M. 5-cincta.* The sex ratio under normal field conditions is exceedingly variable and has been found by Brunson (1934, '39) to depend on the size of the host grubs attacked. Thus 96.5 per cent of the progeny of *T. popilliavora* that develop upon second-instar grubs or *Popillia japonica* are of the male sex, whereas 67.2 per cent of those upon third-instar grubs are females. The stage of development of the host in the field at the time the parasite is active is thus reflected in the sex ratio of the parasite progeny. The female places male eggs upon small grubs and female eggs upon the larger individuals. The above species, when parasitizing *Popillia* grubs in the United States in August, produces approximately 72.3 per cent male progeny, whereas ovipositions during September and later result in 59.2 per cent female progeny. The host oviposition period is largely during July so that very few grubs are in the third instar before September.

Life Cycle.—The great majority of the *Tiphia* occurring in temperate regions have only a single generation each year, though a portion may persist in the cocoon stage until the second year if adverse conditions are encountered. An occasional species produces a second generation. In the more tropical sections, the generations follow without interruption except for periods of estivation due to arid conditions. The incubation period usually covers 3 to 5 days and the larval feeding period 10 to 18 days at summer temperatures. In multibrooded forms, the cocoon stage of the summer generation is complete in 30 to 36 days. The minimum time from egg to cocoon formation is 13 to 15 days in the case of *T. asericae* A. & J. *Myzine 5-cincta, M. haemorrhoidalis,* and *M. ephippium* require only 2 and 5 days, respectively, for the egg and larval stages, and their habits are thus more comparable with those of the Scoliidae than with those of *Tiphia.* In *Pterombus cicindelicidus,* the egg, larval-feeding, and cocoon stages cover 2, 4 to 5, and 22 days, respectively.

So far as known, all species of the family occurring in the temperate regions pass the winter within the cocoon, and most of them are in the larval stage. Several species are in the adult stage within the cocoon, with a few individuals as advanced pupae. Species which emerge early in the spring, such as *T. asericae, T. malayana* Cam., *T. matura* A. & J.,

and *T. vernalis* Roh., hibernate in this way, while those which emerge in the summer and autumn are in the larval stage. *T. femorata* is said to be in the pupal stage during the winter.

IMMATURE STAGES

The egg has been described adequately only for the genus *Tiphia*. The range in size is approximately 1.0 to 2.0 mm. in length, and the width is one-third the length. The eggs are consequently slightly broader in proportion to length than are those of the Scoliidae, and the chorion is considerably heavier. They are uniformly white in color when deposited but quickly assume an amber hue of varying depth, due largely to the oxidation of the mucilaginous material with which they are coated. The coloring becomes slightly more pronounced as incubation proceeds. In a few species, such as *T. agilis* Smith and *T. phyllophagae* A. & J., this darkening is extreme, becoming almost black; other species show various gradations of brownish-black and gray.

In spite of the extensive studies that have been made upon members of the genus, no detailed description has been presented of any of the five larval instars. The segmentation is distinct in all instars of *Tiphia*, but less so in *Myzine* and *Pterombus*, and the thoracic segments are not attenuated as in the Scoliidae. The mandibles of the mature larvae of this family, at least of the genus *Tiphia*, may be distinguished by the possession of a small supplementary tooth at the basal margin of the third of the main teeth. According to T. R. Gardner, there are nine pairs of spiracles, situated on the first thoracic and the first eight abdominal segments, in all instars.

METHOCIDAE

The genus *Methoca* is of world-wide distribution and, so far as known, is parasitic solely upon the larvae of Cicindelidae. The account published by Williams (1919) of a Philippine species, *M. striatella* Williams, illustrates well the habits of the group. The females of this and other species are very ant-like in general appearance and lack wings. The males, on the other hand, are much larger and more robust and possess fully developed wings.

The female *Methoca* searches out the vertical burrow of the host in the soil, within which the larva is lurking and awaits its ascent to the entrance (Fig. 141). The tiger-beetle larva is many times larger than the parasite and is equipped with formidable jaws. Apparently, the normal procedure in attack is for the parasite to permit herself to be seized by the larva, whereupon the sting is quickly inserted in the throat or thorax. In other instances, however, she descends to the larva in the burrow, brings the ovipositor forward beneath the body and inserts it by a quick thrust, or she may enter the burrow backward and sting in that position. Complete and permanent paralysis of the host ensues. A short time may then be spent by the parasite in pinching the ventral portion of the abdomen with the mandibles, following which the egg is deposited longitudinally on the ventral surface of the third or fourth abdominal segment. After this is accomplished, the burrow is filled with soil.

The egg is 1.0 mm. in length, cylindrical, slightly curved, and narrower at the posterior end. Incubation is complete in about two days; after hatching, the young larva feeds first through a minute puncture in the skin, and later the head and a portion of the thorax are buried in the wound. Feeding covers a period of only five or six days, and, owing to the great size of the host, the body contents may not be entirely consumed. The cocoon, which consists of a compact inner layer and a light outer envelope, tapers posteriorly and at the anterior end the outer covering has a wide flaring mouth. The inner cocoon has a constriction at the base of the collar, which is united with the flaring mouth. The host remains may often be found within this "cup." Ten to twenty days may elapse in the cocoon stage, and the cycle is consequently complete in less than one month.

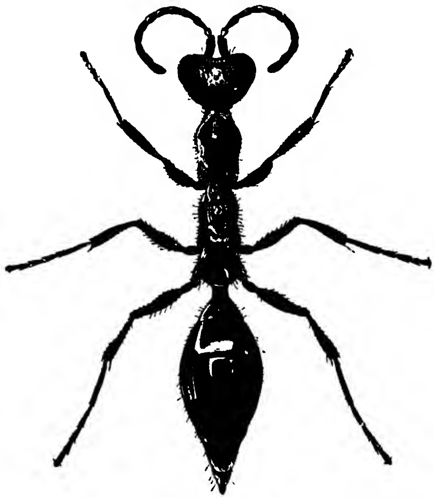


FIG. 140.—The adult female of *Methoca striatella* Williams. (*From Williams*, 1919.)

The habits of the European *M. ichneumonoides* Latr. have been studied by a number of investigators, including Adlerz (1905), Champion (1914, '15), Pagden (1926), and Main (1931). Its habits are essentially similar to those of *M. striatella*, though in oviposition the normal procedure, as first determined by Adlerz, is for the female to permit the host to seize her head or thorax between the mandibles, whereupon the sting is inserted in the throat. The egg is placed obliquely behind and on the inner side of the base of the hind leg. *M. styga* Say places its egg in the same position, whereas *M. punctata* Williams places it longitudinally on the underside of the third abdominal segment, with the anterior end directed forward.

Iwata (1936) has recently studied two species of the genus which show certain differences in habit from those already described. In the case of *M. japonica* Yasum., the preliminary stinging in the burrow is accomplished in the same way; but the paralyzing effect is not so rapid, and the victim usually rushes out of the burrow. It is then stung again, possibly several times, and is dragged back into the burrow, after which the egg is deposited in a diagonal position behind one of the hind coxae. Paralysis is complete but not permanent, and the larva revives and resumes its normal activities.

Parthenogenetic reproduction has been noted in several species, and in each case the progeny were males only.

MUTILLIDAE

The Mutillidae, or velvet ants, are thus termed because of the resemblance of the females to ants and the heavy coating of fine hairs that clothe the body. The males are larger than the females and are usually winged, whereas the latter are apterous. There is an exceptional range in size among the adults of a given species, due to the varying amounts of food available to the individuals during the larval stage.

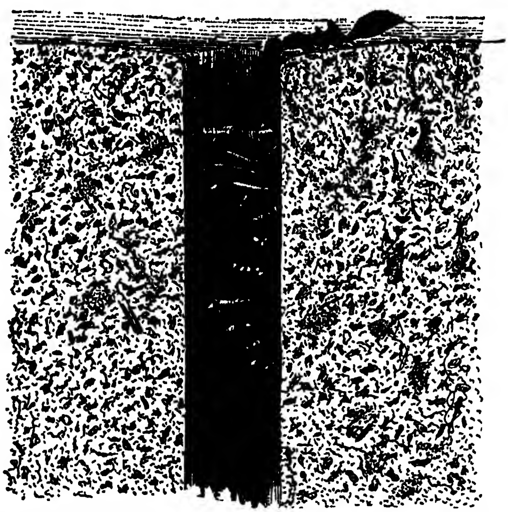


FIG. 141.—A female of *Methoca striatella* Williams about to attack a tiger-beetle larva. (*From Williams*, 1919.)

Mickel (1928, '33) summarizes the known host preferences and habits of the members of the family. The hosts of less than fifty species are known, and the great majority are solitary external parasites upon the larvae, prepupae, and pupae of apoid, vespoid, and sphecoid Hymenoptera. A few species attack Coleoptera (Chrysomelidae; *Clythra* spp. living in ant nests) and Diptera (Muscidae). It appears that the family as a whole must be regarded as predominantly injurious, inasmuch as the greater portion of the insects attacked are themselves predaceous or parasitic upon other insects. In addition, the habit of attacking honeybees is well-known.

Only fragmentary information is available regarding the life histories and habits of the various species. When attack is upon immature Hymenoptera, it is most frequently the inactive mature larva or prepupa in the cell or cocoon that attract the females for oviposition. Mickel

calls attention to this fact and comments on the possession of a powerful sting by the females. Practically all parasitic and predaceous Hymenoptera that are able to sting utilize this weapon in overcoming the host, and they produce either temporary or permanent paralysis. In the Mutillidae, it is probable that the host is stung only if the probing of the ovipositor produces an appreciable muscular reaction, and in any case it serves little purpose. In several species, the removal of the egg from the host has been followed by normal development of the latter. The sting functions largely for defence against adult hosts in the nest or, during the search for food, in direct attack upon adults. This sting is decidedly painful to human beings; Bouwman (1909) tells of the belief among the residents of Cyprus that it is fatal and that many of the English soldiers were killed in this way during the occupation in 1878.

Evidence that the Mutillidae attack adult honeybees was first presented in 1870, the report coming from Texas. In 1878, Schoenfeld recorded the destruction in Austria of as many as 200 bees in a hive in a single day by what was probably *Mutilla europa* L. Only females were found in the hives. In the following year, Scholz recorded similar damage and stated that death of the bees resulted from bites on the back of the neck, after which the body fluids were sucked out. This is at variance with Schoenfeld's statement that the bees were killed by stinging. Although the above species is best known for its injury to honeybee colonies, yet it is not parasitic upon the larval forms of that insect but develops instead upon *Bombus* spp. Hoffer (1886) states that the female pierces the cell, paralyzes the larva, and deposits the egg upon it. A cocoon is spun within the host cell.

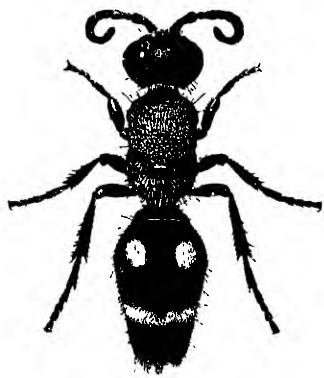


FIG. 142.—The adult female of *Mutilla* sp. (*From Williams*, 1919.)

The habit of attacking adult bees for the purpose of feeding on their body fluids is strikingly illustrated in the case of *Ephutomma continua* F. in Egypt (Mellor, 1927). The host, *Bembex mediterranea* Hal., is usually found in her burrow, about 6 in. below the surface of the sand, during the late afternoon and night. The female *Ephutomma* is crepuscular in habit and searches out the *Bembex* burrows. Apparently no resistance is offered by the host, and no stinging takes place. The predator immediately begins to malaxate the throat of the victim; this may be continued for several hours. Eventually, the thin membranes of the throat and other parts of the body are broken, and the contents are consumed.

In general, the bees are decidedly aggressive in defending themselves and their nest from various enemies, and it is consequently surprising to find, in the above instances, that no effort is made to repel the intruders and no resistance offered even when the individual is attacked directly. This passiveness in the face of invasion or attack is not shown by all hosts, as was determined by Melander and Brues (1903) in their observations upon *Halictus* spp. Upon the approach of *Mutilla canadensis* Blake to the nest, the female watcher on guard rushes out and engages the intruder in combat. If a male is on guard, he merely turns about and blocks the entrance to the nest with his abdomen.

Janvier (1933) gives an account of two species of *Mutilla* that develop upon andrenid bees in Chile. *M. attenuata* Spin. is a solitary external parasite of the pupae of *Halictus chloris* Ill.; the egg is introduced into the cell at the time of transformation of the host to the pupal stage and is placed obliquely across the pronotum. The feeding period of the parasite larva covers about 15 days. *M. lunata* Spin. attacks the mature larva of *Tetralonia tristrigata* Spin. in much the same way.

Several species of *Mutilla* are known to attack the pupae of the tsetse fly in Africa. Lamborn (1915) describes briefly the habits of *M. glossinae* Turn. The female spends 30 minutes or more in gnawing a hole in the puparium; after this is accomplished, the ovipositor is inserted and the egg laid. The puncture is then apparently sealed with a mucilaginous material.

Very little information is available regarding the form or habits of immature stages of the Mutillidae. The egg of *Mutilla* sp. (Williams, 1919*b*) is stated to be elongate and curved, with the chorion minutely granulate. It is placed transversely upon the dorsum of the *Tiphia* larva, between the first and second thoracic segments. The point of larval feeding, however, is ventral. Ferton states that the egg of *Stenomutilla argentata* var. *saundersivora* Fer. is attached to the inner wall of the host cocoon. The early larval instars have not been described for any species. The mature larva of *M. glossinae* has 11 pairs of spiracles, situated on the second and third thoracic and the first nine abdominal segments. The mandibles are 4-dentate, whereas those of *M. lunata* and *M. attenuata* are stated to be tridentate. The mature larvae of all species spin a cocoon within the cell, cocoon, or puparium of the host, though in some instances it is imperfect.

The life cycles of several species are known and range in length from about three weeks to one year. The egg stage covers 3 or 4 days and the larval feeding period 5 to 15 days.

SCOLLIDAE

The family is limited in its host preferences, so far as known, to coleopterous larvae of the family Scarabaeidae and, less commonly,

to the grubs of the larger Curculionidae, particularly of the genus *Rhynchophorus;* all are solitary external parasites. Two genera, *Scolia* and *Campsomeris*, are well-known and are of cosmopolitan distribution. The wasps are of relatively large size, and *Scolia atrata* F. of tropical America, which has a wing expanse of nearly 7.5 cm., is conspicuous also because of its black body color and iridescent wings.

Several attempts have been made to utilize species of this family in the biological control of scarabaeid pests of field crops, but the only instance of a successful outcome was in Hawaii, where establishment of the Philippine *S. manilae* Ashm. was accomplished upon *Anomala orientalis* Waterh. This pest was quickly and fully controlled by the parasite except in certain limited localities where conditions were not favorable for its development.

BIOLOGY AND HABITS

Habits of the Adult.—The flight of many of the Scoliidae is rather characteristic, being on a horizontal plane only a few inches above the ground and following a circular or figure-8 course. The males become active somewhat earlier in the morning than the females, and mating is largely effected upon the surface of the ground or upon low vegetation as soon as the females appear. Rau (1932) states that the females of *Scolia dubia* Say attract the males by spreading the wings so that the brilliantly colored body is revealed. This general flight of both sexes is completed early in the afternoon, when the males become quiescent and the females enter the soil in search of grubs for oviposition.

In several species, the swarming habit of the males has been noted to occur quite generally. Males of *Campsomeris dorsata* F. of the West Indies congregate in large colonies, numbering several hundred individuals, upon foliage and remain quiescent during the night. Rau states that the unmated individuals of both sexes of *S. dubia* have this habit; but after mating the gregarious habit is abandoned, and the night is passed beneath rubbish. In general, the females of the family are solitary and pass the night in the soil.

The food of adult Scoliidae consists chiefly of nectar derived from the blossoms of various plants, particularly of the Umbelliferae, but also from a great variety of others, ranging from sweet potato to orange. Illingworth (1921) mentions that the adults of *Discolia soror* Smith feed extensively on the secretions of leaf hoppers, but this is the only known instance of honeydew feeding by adults of this family.

In locating the host grubs for oviposition, the female is under the necessity of burrowing extensively in the soil, and she doubtless often utilizes the burrows that the grubs themselves have made. During their feeding period, the scarabaeid grubs are usually only a few inches beneath the surface and are located without great difficulty; but Janvier (1933)

mentions that females of *Cosila chilensis* Guer. penetrate to a depth of 40 cm. to reach the host grubs. The females of *Campsomeris dorsata* frequently attack *Ligyrus* grubs upon the surface of the soil. This is true also of *S. dubia* upon *Cotinus* grubs, which are frequently found upon the surface of the ground during the early morning hours.

The stinging of the grub under natural conditions in its cell in the soil is accomplished by curling the body transversely about it and inserting the sting several times in the thoracic region. According to Illingworth, the procedure is somewhat different in the case of *Campsomeris radula* F., at least upon the surface of the soil; for the wasp first grasps a mandible from the front and then inserts the sting just anterior to the front coxae and then into the throat. Corbett describes a similar

FIG. 143.—The adult female of *Campsomeris annulata* F. (*From Clausen et al.*, 1927.)

habit in *C. javana* Lep. and *C. pulchrivestita* Cam. and states that the females utilize both the mandibles and the tip of the abdomen in an extensive kneading and manipulation of the host body. This habit has not been noted in other members of the family. Complete and permanent paralysis normally results from the sting. The one exception to this rule is *S. formosa* Guer. the host grub of which is stated by Tryon (1902) to continue feeding for a time after being attacked. Various writers have pointed out that the scoliid females sting a considerably larger number of grubs than they are capable of successfully parasitizing. This results in a proportionate increase in effectiveness, for the grubs that are stung but that do not receive an egg never recover.

After the grub is completely paralyzed, the wasp then burrows deep into the soil, dragging the grub behind it, and, at a depth of 25 cm. to as much as 1 m., a cell is formed within which the grub is placed and the egg then deposited. The depth to which the parasite penetrates with its victim depends largely upon the nature of the soil; in sandy

places, the parasitized grubs are found at a greater depth than in clay or loam. This burying of the host grub at a considerable depth provides much more uniform temperature and humidity conditions for the development of the young parasite.

From the limited information available, there appears to be some variation among species in the manner of deposition of the egg. This is concluded from the position of the egg, for direct observations are not possible under natural conditions. In practically all species of the family, the egg is placed perpendicularly upon the median ventral line of the third or fourth abdominal segment. Those of *Campsomeris javana*, *C. pulchrivestita*, and *C. trifasciata* F. have the concave ventral side facing cephalad, and the wasp must consequently have been oriented in the same way as the host at the time of oviposition. In *S. japonica* Smith, *C. annulata* F., and *C. dorsata*, the eggs are in the reverse position, and the wasp accordingly was facing caudad. In *Cosila chilensis*, however, the egg is placed upon the upper side of the body and lies horizontally rather than standing upon one end.

In the majority of species of *Scolia* and *Campsomeris*, the egg is lightly attached by its posterior end to the body of the host, and at hatching the body of the young larva is bent forward and the feeding puncture made one segment preceding or following that which bears the egg, depending on whether the venter of the egg faces cephalad or caudad. In the case of *S. manilae* (Williams, 1919*b*) and *S. hirta* Schr., it is stated to be attached by the anterior end, a position that would require considerable manipulation of the egg by the female at the time of deposition.

Larval Development.—The habits of *C. annulata*, parasitic upon the grubs of *Phyllophaga* and *Anomala* in the Far East (Clausen *et al.*, 1933), may be given as representative of the family. At hatching, the chorion is broken over the head and thoracic segments, and the fore part of the body of the larva then emerges. The larva bends forward and is soon able to make a feeding puncture on the median line of the segment preceding that bearing the egg. Very shortly thereafter, the body is removed entirely from the eggshell and lies either longitudinally or diagonally upon the host body. At first only the head of the parasite larva is embedded in the feeding puncture; but after the first molt the body is penetrated more and more, until the thoracic segments, which are considerably elongated and narrowed, are within the body. The puncture at this time is slightly less than 2.0 mm. in diameter, and there is a marked exudation of body fluids, which appears as a liquid ring about the neck of the larva. Early feeding is largely in the anterior portion of the body; but later the position is reversed, and the entire contents are consumed, though none of the integument is eaten.

Illingworth mentions that the larvae of *C. radula* have the habit of ejecting water at intervals from the tip of the body, the jet being projected 15 cm. or more. This is doubtless an adaptation for the elimination of waste products. The meconium of all species, so far as known, is cast by the mature larva or prepupa after the formation of the cocoon. It is in fluid form and is completely absorbed by the porous cocoon wall.

There is some variation in the form of the cocoons spun by different species. The cocoon of *C. annulata* is reddish-brown in color, has a thin wall consisting of a single layer, and is enveloped in a considerable mass of loose threads. It is broadest at the anterior end, but both ends are smoothly rounded. That of *S. japonica* has a somewhat glazed surface and lacks entirely the mass of loose threads above-mentioned. The cocoon wall is usually delicate, though in *Cosila chilensis* it is compact and strong.

Cocoons from which the adults have emerged have a circular cap smoothly cut out at the anterior end and may be distinguished readily from those of the Tiphiidae by this means. In the latter family, the emergence hole is smaller, situated slightly to one side at the anterior end, and the edges of the hole are irregular.

Reproduction.—The reproductive capacity of the Scoliidae is relatively low, judging from the few records available. Williams records the deposition of 52 eggs in a period of 79 days by *S. manilae*, and Illingworth secured a maximum of 95 eggs from *C. tasmaniensis* Sauss., these being deposited over a period of 70 days. Under optimum conditions, the females are able to deposit 2 eggs per day, though this average is seldom maintained. In the first-named species and in *C. radula*, also, it has been found that unmated females have a slightly reduced reproductive capacity.

Under field conditions, the two sexes are usually present in approximately equal numbers, though the males naturally die earlier than the females and consequently the latter sex predominates during the later portion of the period covered by each brood. Tryon states that in *S. formosa* the females greatly predominate in the spring brood, whereas the opposite is true in the second, which appears in the autumn.

Observations on parthenogenetic reproduction have been largely limited to the Australian species, *C. radula* and *C. tasmaniensis*. Illingworth found that unmated females of these species produce male progeny, though an occasional female is interspersed among them. Box (1925) also records the appearance of occasional females of *C. trifasciata* among the progeny of virgin females.

Life Cycle.—In temperate regions, the majority of Scoliidae have only a single generation each year, though in Chosen *C. annulata* has two

or three, and adults are present in the field from May to October. There is no obligatory resting period, however, and the generations succeed each other at intervals of about six weeks as long as conditions remain favorable. The developmental period is greatly prolonged at reduced temperatures. The incubation period of most species under optimum conditions covers two or three days, though in *Scolia japonica* it is completed in a single day. The larval period, to the spinning of the cocoon, is 6 to 9 days, with a minimum of 4 days for the above species. The cocoon stage for the summer generation ranges from 30 to 40 days. *C. annulata* requires only 5 days for larval development and 21 days for the cocoon stage. Most species probably pass the winter in the mature larval stage within the cocoon, though hibernating cocoons of *C. annulata* were found to contain pupae and there were some indications that a portion of the adult females present in the field during the autumn may survive until the following spring.

IMMATURE STAGES

The eggs of the different species range in length from about 2.0 mm. to the 4.0 mm. of the enormous *S. oryctophaga* Coq. of Madagascar. They are about one-fourth as wide as long, with the anterior end slightly the wider; both poles are smoothly rounded, the ventral side is almost straight, and the dorsum is slightly convex. The chorion is unornamented, thin, and transparent.

Very little detailed information is available regarding the characters of the larvae. There are four larval instars, which do not differ in general appearance, though in the instars following the first the anterior segments of the body are long and narrowed. There are no visible integumentary spines or setae. The mandibles of the first instar are simple, and those of the following instars are tridentate. The mature larva has 10 pairs of spiracles, situated on the last two thoracic and the first eight abdominal segments.

FORMICIDAE

The ants have a great variety of food sources, ranging from fungi, plant sap, exudations or seed, and honeydew secreted by various insects up to an exclusively carnivorous diet. Their value in a predatory capacity is perhaps generally underestimated. Phillips (1934) mentions that the housefly in Hawaii is held down to negligible numbers by the accidentally introduced *Pheidole megacephala* F., and the increase and spread of many other pests are prevented. Experiments by Pemberton and Willard (1918) indicate that approximately three-fourths of the population of the Mediterranean fruitfly succumb to attack by this species after the larvae are mature and reach the ground. The habits of the driver and legionary ants of the tropics have been described by various authors. These, when on the march, destroy not only all insect life that is unable to escape by flight, but even the higher forms of animal life as well. For detailed accounts of the habits of the family and their

relations with other insects, the reader is referred to the extensive writings of Donisthorpe, Emery, Escherich, Forel, McCook, Wasmann, and Wheeler.

Ants were the first group of insects utilized in an attempt to control insect pests by the biological method. For centuries, the date growers of Yemen have brought ant colonies from the hills and placed them in the trees for protection from other ant species that were causing much damage. In south China, many citrus growers collect the nests of *Oecophylla smaragdina* F., place them in the trees, and even provide bamboo runways for them between the trees (Groff and Howard, 1924). This ant is stated to destroy all kinds of caterpillars except the hairy species and to drive away beetles and various bugs, thus preventing oviposition. Another ant, *Dolichoderus bituberculatus* Mayr, is employed in Java for the protection of cacao plantings from injury by *Helopeltis*.

One of the most efficient groups of predaceous ants is the genus *Solenopsis*. It is recorded that 75 per cent of the larvae, pupae, and adults of the southwestern corn borer, *Diatraea grandiosella* Dyar, are destroyed by *S. geminata* var. *diabolica* Wheeler.

BETHYLIDAE

The members of the family Bethylidae attack almost exclusively the larvae of Lepidoptera and Coleoptera, thus showing an exceptional uniformity in host preferences. The lepidopterous hosts are very largely the grain and flour moths, leaf miners, leaf rollers, case bearers, and shoot and fruit borers. The beetle hosts comprise various species that infest stored grains and legumes and their various products and other stored plant materials, and, in addition, the bark- and wood-boring Scolytidae, Cerambycidae, and related groups. The records of attack upon Hymenoptera, of which there are several, must be considered as doubtful, inasmuch as none of them has yet been established beyond question. The hosts are usually contained in a cell of some sort, such as a burrow, tunnel, leaf roll, feeding chamber, or cocoon, and attack upon exposed hosts seldom occurs. Development is always external, and the great majority of species are gregarious.

In some genera and species, it is difficult to correlate the sexes, for although the females are usually apterous, or occasionally subapterous, and the males winged, in others both winged and apterous forms appear in both sexes. In *Sclerodermus immigrans* Brid. and *S. macrogaster* Ashm., one-third of the females are winged and only a small fraction of 1 per cent of the males are apterous (Bridwell, 1929). Wheeler (1928), in discussing the latter species, states that the winged females and wingless males are rare. About one-fourth of the males of *Cephalonomia gallicola* Ashm. are apterous (van Emden, 1931), while the winged forms

are said to predominate in *C. hypobori* Kieff. Kearns (1934*b*) found that some virgin females of *C. gallicola* produce both winged and wingless male progeny in approximately equal numbers, whereas others produce males of one form or the other but not both. The females of *Epyris extraneus* Brid. (Fig. 144) of Hawaii and the Orient are normally alate.

In view of its attack upon a number of serious lepidopterous and coleopterous pests, the family is distinctly beneficial. Occasional exceptions occur, such as the species of *Parascleroderma* that are parasitic upon the predaceous clerid beetle, *Thanasemus formicarius* L.

Very few representatives of the family have been utilized in biological control work, the best known being *Prorops nasuta* Waterst. from Uganda,

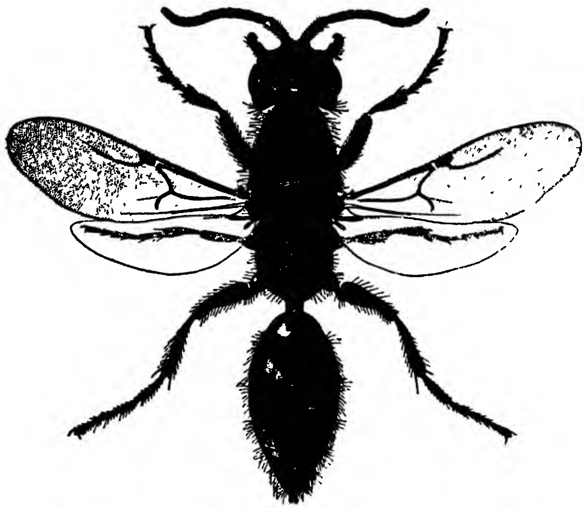


FIG. 144.—The adult female of *Epyris extraneus* Brid. (*From Williams*, 1919.)

which has been colonized against the coffee borer, *Stephanoderes hampei* Ferr., in Brazil and Java. An appreciable reduction in the infestation in Brazil is reported as a result of this introduction.

BIOLOGY AND HABITS

The Bethylidae are of interest in several respects, particularly because of their mating and food habits, the maternal care of the brood, and a tendency in several species toward community life. Extended summaries of the habits of the family have been presented by Bridwell (1919, '20) and Wheeler (1928), but the most thorough study of a species is that by van Emden (1931) upon *Cephalonomia galliçola* Ashm., a gregarious external parasite of the larvae and pupae of the anobiid beetle, *Stegobium paniceum* L., in Europe. Kearns (1934*a*) has studied the same species as a parasite of the cigarette beetle, *Lasioderma serricorne* F., in North America.

Habits of the Adult.—In the gregarious species of the family, the males of the brood normally emerge somewhat in advance of the females; they have the habit of then tearing open the female cocoons and, often, of entering them in order to mate with the newly transformed females. This habit of the males of assisting in the emergence of the females results in very extensive inbreeding; in fact, this is normal in many species. Its effects, however, are offset by the repeated mating that is necessary during the life of the individual females, and the matings following the first are, in most instances, with males of unrelated broods. The closest inbreeding occurs in the species that are able to produce several successive broods upon a single host individual. Under such circumstances, a female may mate with males of several generations of her own descendants.

The behavior of the adult female in her attack upon the prey, the method of feeding, and finally the tendency toward maternal care of the progeny are distinctive. In the initial attempt to overcome the host larva, the female parasite usually crawls over the dorsum and curves her abdomen beneath the thorax, inserting the sting first in the throat or in one of the thoracic segments. This apparently is for the purpose of paralyzing the mandibles and legs. In *Sclerodermus chilonellae* Brid., however, the initial stinging is by a backward thrust toward the mouth. Repeated stinging takes place, the later insertions being in the abdominal region. In *Laelius anthrenivorus* Trani, the female then chews the throat, apparently with the object of injuring the cervical ganglion. The complete process of subduing the host may require several hours.

A number of species have the habit of attacking the host in the open; after stinging, they transport it to a suitable crevice or cavity, after the manner of the fossorial wasps. *Bethylus fulvicornis* Curt. stores its caterpillar victims in hollow stalks. The host, being usually considerably larger than the parasite female, is dragged along the surface, though *Epyris extraneus* Brid. and *Cephalonomia mycetophila* Kieff. carry it across the dorsum. Paralysis of the host is usually complete and permanent, though in the above species and in several species of *Goniozus*, it is only temporary and of one-half to two hours' duration.

Feeding by the adult female upon the body fluids of the host is a general habit in the family, and this type of food is apparently essential for egg development, as is indicated by the frequent lapse of several days between such feeding and the deposition of the first eggs. In many species, the female spends her entire life in the burrow, cell, or cocoon of the host, and under these circumstances the body fluids are the only food available to her. Females of the genus *Laelius* have not been observed to feed upon the host. According to Bridwell, all members of the *Goniozus* group require sugary foods, *Sclerodermus* feeds only

on the host fluids, and the *Epyris* group feed upon both materials. The preoviposition period has been found to cover a minimum of five days. The number of hosts which are attacked and paralyzed by a female is often considerably in excess of that which receive eggs. Ramachandra Rao and Cherian (1928) state that females of *Perisierola nephantidis* Mues. were observed to mob full-grown caterpillars and kill them. In the case of *Prorops nasuta*, the female often feeds upon young coffee-borer larvae, though oviposition takes place entirely upon mature larvae. It appears that the total host mortality effected by members of this family may be considerably in excess of that resulting from successful parasitization. The females of the genus *Laelius*, which attack the larvae of Dermestidae, bite away the covering of long hairs on the venter of the abdomen before depositing their eggs (Howard, 1901).

Complete and permanent paralysis of the host is the general rule in the family. An exception is *Goniozus* sp. (Taylor, 1933), which parasitizes *Nacoleia octosema* Meyr. in Java. The caterpillar recovers from the sting and continues its normal activities until the hatching of the parasite eggs, when it spins a scanty cocoon. The caterpillar host of *G. claripennis* Foerst. (Voukassovitch, 1925*b*) also recovers within two hours after being stung and may molt, though this is usually inhibited. In this species, also, a light cocoon may be spun before death.

The position of the egg upon the body of the host is variable, though there is some uniformity within genera. The eggs of the solitary species are found lying longitudinally, with the anterior end directed caudad. The egg of *Prorops nasuta* is ventrally on the thorax; that of *Parascleroderma berlandi* Man. (Maneval, 1930) is attached at the side; in the case of *E. extraneus*, the egg is on the venter of the first abdominal segment, and in *Holepyris hawaiiensis* Ashm. it is upon the dorsum of the posterior portion of the abdomen. Among the species of gregarious habit, the eggs are usually placed transversely, exceptions to this rule being *Perisierola gallicola* Kieff., whose eggs lie longitudinally on one side of the dorsum, and *Laelius* spp., which deposits them in two rows upon the venter of the abdomen. *Cephalonomia gallicola* Ashm. and *Bethylus cephalotes* Foerst. place them in two rows on the venter of the abdomen of the host larvae, but in the case of *Cephalonomia* the position is changed to the intersegmental grooves of the dorsum when the pupal stage of the host is attacked. *C. mycetophila* Kieff. differs in habit from other species of the genus in placing its eggs upon the dorsum of the thorax of the host larva. An interesting variation is found in *C. tarsalis* Ashm., which is parasitic upon *Oryzaephilus* larvae. Only two eggs are placed upon each host; the first one deposited, which is destined to develop into a female, is placed upon the side of the prothorax, and the second, which is consistently a male, is deposited upon the mesothorax (Powell, 1938).

Several species of *Goniozus* deposit their eggs transversely in the intersegmental grooves of the mid-dorsal region.

The egg positions mentioned above indicate several variations in the manner in which the females accomplish oviposition. In the species that place the eggs longitudinally with respect to the host body, the female must take the venter-to-venter position during the act, whereas those which place the egg transversely in an intersegmental groove encircle the body of the host in a manner identical with that of the Tiphiidae.

There is considerable evidence that the females of the different gregarious species regulate, somewhat in relation to its size, the number of eggs deposited upon a single host. *Perisierola emigrata* Roh. deposits only two eggs upon small *Ereunetis* larvae and an average of about eight on the larger larvae of *Cryptophlebia.*

The total number of eggs deposited by a single female ranges up to a maximum of 150, though Willard (1927) records 236 from one female of *P. emigrata* in 44 days. A female of *Cephalonomia gallicola* deposited 158 eggs upon 76 hosts during a period of 36 days; in addition, 42 *Lasioderma* larvae were killed but not parasitized (Kearns, 1934). Mated females of *C. tarsalis* deposit an average of about 85 eggs, whereas virgin females produce only 50. The solitary species probably produce a smaller number. In the gregarious species, an interval of several days usually elapses between the deposition of successive batches of eggs.

Larval Development.—The newly hatched larvae are virtually incapable of movement and consequently make their feeding punctures and fix themselves before they are completely freed from the eggshell. A single feeding puncture is used throughout the life of the larva. In the late first stage, the larva of *Goniozus claripennis* is U-shaped, with a fold of host skin firmly held between the two ends of the body, thus anchoring it firmly in position. In the intermediate and late larval stages of *Laelius anthrenivorus*, the head and thoracic segments are embedded in the wound, and often more than half the body of the larva is within the host. During the first portion of the feeding period, the larva lies horizontally upon the body of the victim; but as development proceeds the parasite body becomes more spindle-shaped, and, in a number of species and genera, it assumes a vertical position (Fig. 145). This usually does not occur until the last stage. The larvae which lie in the horizontal position retain the exuviae as a pad beneath the body, whereas those which stand vertically carry them at the posterior end of the body. The "irregular shield of rugose lemon-yellow skin bearing two hairs" mentioned by Hyslop (1916) for *Pristocera armifera* Say is probably a cast skin.

Maternal care of the developing progeny is exhibited in a number of species, ranging from attention for only a few days after oviposition in *C. gallicola* up to the completion of larval development in *S. immigrans* and *S. macrogaster*. Wheeler mentions that the females of the latter species often stand over the brood and lick their bodies, at which time they are held between the forefeet. They will at times eat their own eggs, though not their larvae, and this habit is believed to be associated with a tendency toward regulation of the size of the brood rather than being the result of a shortage of food.

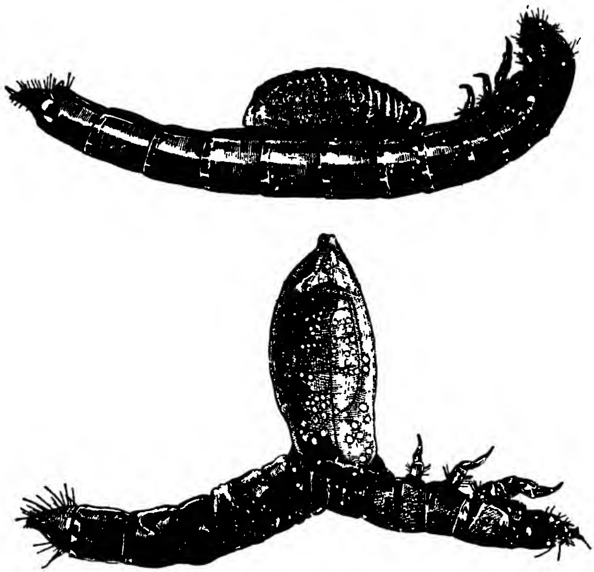


FIG. 145.—Successive stages in the feeding of a larva of *Epyris extraneus* Brid. upon a larva of *Gonocephalum*. (*From Williams*, 1919.)

Bridwell mentions that occasionally several females of *Sclerodermus* were observed living together and rearing their progeny upon a single host larva, and without any indications of interference or cannibalism, even though the females were, in some instances, of different species.

The larval feeding period is exceptionally short, being complete in 2 to 3 days in several species of *Goniozus* and *Cephalonomia*, while the majority probably require about 5 days. The maximum duration of this period is the 10 days required by *B. cephalotes*.

In contrast to the younger larvae, those which have completed development are quite active and are able, in some species, to move several centimeters away for pupation. Practically all species spin cocoons, which in the gregarious species, are usually matted together. *Parasclero-derma berlandi* spins a transverse operculum across the burrow of the

host prior to forming the cocoon. An unusual pupation habit is recorded for *Perisierola* sp., parasitic upon the larva of the strawberry leaf roller, *Ancylis comptana* Froel. in North America (Fink, 1932). No cocoon is formed, but the mature larva fastens the tip of its abdomen to the leaf surface and then transforms to a pupa within the last larval skin, which becomes jet black in color.

There is a considerable variation in size among the individuals that develop upon a single host, due largely to crowding. Where the number of eggs deposited is appreciably above that which can be brought to maturity, the surplus larvae succumb, presumably by being forced away from the available food supply.

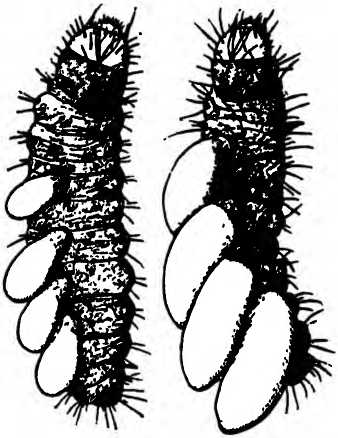


Fig. 146.—Caterpillars of *Tmetocera* bearing larvae of *Perisierola gallicola* Kieff., those at the right being nearly mature. (*From Silvestri*, 1923.)

Life Cycle.—The life cycles of the various Bethylidae that have been studied range from 9 to 12 days as a minimum to a more frequent period of 30 to 35 days. *C. gallicola* requires 34 days at 22.6°C. and 64 days at 18.4°C. *S. domesticus* Kieff., however, is said to require at least two months for development. The egg stage covers 1 to 4 days, with an extreme of 7 days in the case of *Parascleroderma berlandi*, though that of *C. gallicola* extends to 13 days at the minimum temperature given above. The larval feeding period is usually followed by a rather prolonged resting period in the cocoon prior to pupation. The time spent in the cocoon usually ranges from 10 to 20 days, though *Perisierola nephantidis* on *Nephantis serinopa* Meyr. in India is stated to require only four days (Ramachandra Rao and Cherian, 1928). In *C. gallicola,* according to Kearns, the females, winged males, and apterous males require 11 to 18, 9 to 15, and 7 to 12 days, respectively, in the cocoon. Adult life of the females ranges from one to three months under summer conditions with hosts available for feeding and reproduction. The life of adult males is much shorter, being only 6 days in the case of *C. tarsalis,* and no feeding takes place during this period. The winter may be passed either in the adult stage in sheltered places or in the mature larval or pupal stage in the cocoons. In a number of species, two generations are produced during the time required for one of the host.

Sex Ratio.—The females predominate numerically in all species in which data relating to the sex ratio have been secured. This ranges from 2 to 1 in *S. domesticus* to 5 to 1 in *S. immigrans*. In a series of rearings of

S. immigrans, Keeler (1929*a*, *b*) secured only female progeny from unmated females and found that wingless females produced that form only. In contradiction to this, Bridwell (1929) records that his own extensive rearings from virgin females of the same species resulted only in males. Keeler's rearing technique appears to preclude the possibility that mating may have occurred inadvertently. On the basis of these studies it appears that two biological races may be involved, and it is particularly surprising that thelyotoky should have developed in a race or strain of one species and not occur elsewhere in the family. Taylor found that the brood of three to five *Goniozus* sp., which develops upon the larva of the banana scab moth, usually includes a single male. Wheeler (1928) states that oviposition by virgin females of *S. macrogaster* is conspicuously delayed, and Soika (1932) asserts that parthenogenetic reproduction cannot occur in *S. domesticus.*

IMMATURE STAGES

Though extensive observations have been made upon the habits of a number of species of the family, yet in no instance have the early stages been adequately described.

The eggs of the different species are quite similar, being elliptical to elongate-ovoid, 0.3 to 1.5 mm. in length, and two to four times as long as wide. Usually, they are slightly curved, with the anterior end broader. The chorion is smooth and glistening except in *Prorops nasuta,* which has a granulate or reticulate surface.

The first-instar larva of *Perisierola gallicola* (Fig. 147) is robust, with the segmentation indistinct. The head is large and nearly hemispherical. There are eight pairs of spiracles, situated on the first and third thoracic and the first six abdominal segments.

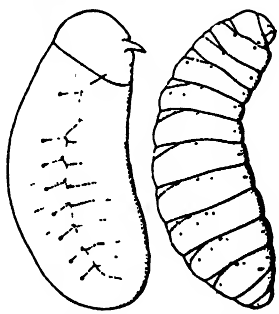


FIG. 147.—The first-instar (at left) and mature larvae of *Perisierola gallicola* Kieff. (*From Silvestri,* 1923.)

The number of larval instars is known for only a few species. Williams (1919*a*) records four for *Epyris extraneus,* and five are described for *Cephalonomia gallicola* and for *Laelius anthrenivorus* (Vance and Parker, 1932).

The larval instars show little variation in their general characters. The early instars are usually indistinctly segmented and often pyriform, with only the main body divisions indicated. The third-instar larva of *C. gallicola* bears a pair of long setae on the median ventral line of the first thoracic segment. The mature larvae are usually unornamented, with the integument thin and transparent. In *P. gallicola,* however, there is a transverse band of backwardly directed papillae on each thoracic segment, and a few fine hairs on the abdomen.

The mandibles are also an extremely variable character, though they are large and protruding in all species. In *E. extraneus,* they are simple in the first instar, bidentate in the second, and tridentate in the third and fourth instars, and those of the successive instars of *L. anthrenivorus* have two, two, three, five, and seven teeth. In *P. gallicola,* they are simple in the mature larva, and presumably in the early instars, also.

The number of spiracles is decidedly variable among the different species. *P. gallicola* (Silvestri, 1923*b*) has eight pairs in the first instar, situated on the second

thoracic and first seven abdominal segments, and on the mature larva additional pairs appear on the third thoracic and eighth abdominal segments. *B. cephalotes* (Richards, 1932) also has eight pairs in the first instar. In contrast to this, *L. anthrenivorus* has a single pair on the second thoracic segment in all instars, and *C. gallicola* and *C. tarsalis* have five pairs in all instars.

The cocoons are oblong or somewhat cylindrical in form and tough and firm. In *E. extraneus*, the anterior end is less firm and is closed off by a neat disk, which is cut away at the time of adult emergence. The cocoons of *P. emigrata* and several other species are white and delicate and may be loosely woven.

DRYINIDAE

The Dryinidae are considered to be closely related taxonomically. to the Bethylidae and are often included as a subfamily of that group. In the subfamily Dryininae, which includes the great majority of species whose parasitic habits have been studied, the females show a remarkable modification in the form of the tarsi of the front legs, which are chelate. This is considered to be an adaptation for seizing and holding the host during oviposition. In the Aphelopinae, however, the tarsi are of simple form. Many species of the family have apterous females, which bear a striking resemblance to ants, and consequently it is difficult to associate the sexes of a species except through rearings or by the capture of mating pairs.

The host preferences of the Dryinidae are exceptionally consistent, for all species are parasitic upon homopterous nymphs and adults of the families Fulgoridae and Cicadellidae, with a single species only upon the Membracidae. From the economic point of view, the value of the Dryinidae in reducing the pest population by parasitization is greatly enhanced by the predaceous habits of the adults. This is apparently quite general in the family, and several authors have expressed the opinion, with respect to particular species, that a greater mortality is effected in this way than by parasitization.

A number of species of the family exert an appreciable effect in the natural control of their hosts, which are often of considerable economic importance. *Haplogonatopus vitiensis* Perk. and *Pseudogonatopus hospes* Perk. were successfully introduced into Hawaii from Fiji and China, respectively, in connection with the biological control of the sugarcane leafhopper, *Perkinsiella saccharicida* Kirk.

BIOLOGY AND HABITS

No complete account has yet been presented of the life history and habits of any member of the family. Fragmentary data are available regarding a number of species, and these have been reviewed by Perkins (1905*a*) and Fenton (1918). The latter describes and figures the different instars of *Gonatopus contortulus* Patt., a solitary parasite of the adults of

Deltocephalus sayi Fitch, and gives biological data regarding several additional species.

Most of the ectoparasitic species may be either solitary or gregarious, though in the latter case the number on each host is small. A high percentage of parasitization of the host results in frequent duplicate oviposition, whereas the chance of this is slight in light infestations. A few species, particularly those attacking early-instar hosts, are consistently solitary, and the food supply is sufficient for only a single individual.

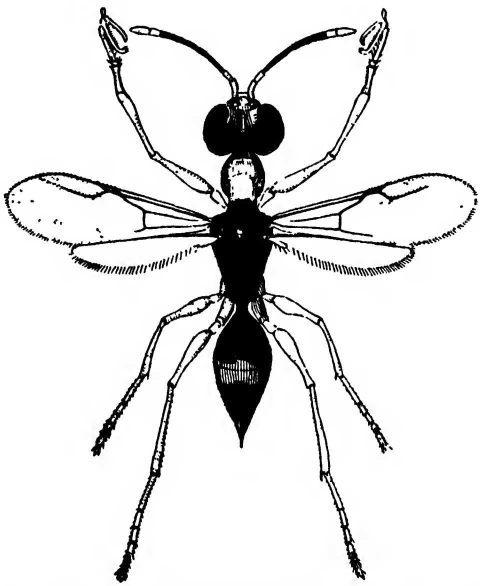


FIG. 148.—The adult female of *Echthrodelphax fairchildii* Perk. (*From Perkins*, 1905.)

Habits of the Adult.—The manner of oviposition and the region of the host body in which the egg is placed vary considerably. In *Aphelopus theliae* Gahan (Kornhauser, 1919), the female grasps the caudal portion of the abdomen of the young nymph of the membracid host, *Thelia bimaculata* F., with her powerful mandibles and with her legs, also, and thrusts her ovipositor through the membrane between two abdominal segments. With fourth- or fifth-instar hosts, she usually clings with both mandibles and legs to a tibia, instead, and inserts the ovipositor through the membrane between the femur and trochanter or at the base of the coxa. After oviposition, the female mounts to the dorsum and feeds upon the drop of honeydew excreted by the host during its effort to escape from the clutches of the parasite.

In the subfamily Dryininae, the females of which possess chelate tarsi, the mode of attack is quite different. The nymphal host is grasped

with the front legs and securely held while the ovipositor is inserted. The female of *Echthrodelphax fairchildii* Perk. jumps upon the back of the host, grasps the neck with the forelegs and the posterior portion of the body with the hind legs, and then inserts the ovipositor beneath one of the wing lobes. *Pseudogonatopus hospes* grasps the legs of the host with the chelae and stings it ventrally in the mesothorax before ovipositing between two of the anterior abdominal segments. The female of *Haplogonatopus japonicus* E. & H. (Esaki and Hashimoto, 1931) seizes the host in her fore legs, lifts it off the leaf, and inserts the ovipositor in the mid-abdominal region. She may also use the mandibles for holding it and may turn it about in order to locate the proper point for insertion of the ovipositor. In general, paralysis resulting from the sting is of very short duration and in some species is entirely lacking. Permanent paralysis and death of first- and second-instar nymphs of *Delphacodes furcifera* Horv. result from the sting of *H. japonicus.*

The stage of the host that is attacked, and the sex also, appear to vary somewhat among the different species. The genus *Aphelopus* quite generally attacks the host in the early instars, and of both sexes. An exception is *A. melaleucus* Dalm. (Keilin and Thompson, 1915*b*), parasitic in *Typhlocyba,* which evidently attacks only adult hosts, for isolated individuals first show the larval sacs as much as a week after capture. No nymphs have been found bearing the larval sacs of this parasite. *Gonatopus ombrodes* Perk. attacks only the adult females of *Cicadula* and *Deltocephalus* (Ainslie, 1920). *P. hospes* attacks preferably the last two instars of *Delphacodes furcifera* (Pagden, 1934), and this is likewise true of *G. erythrodes* Perk.

In all species of the family, the egg is normally placed completely within the host body. Fenton, however, mentions that it may occasionally be placed externally by *G. contortulus* and that in *Gonatopus* sp., parasitic in nymphs of *Deltocephalus inimicus* Say, it is largely embedded in the body, but the anterior end protrudes slightly from the wound. It has not yet been definitely shown that normal development can follow such placement of the egg.

Larval Development.—Although there is some disagreement among authors as to development during the first larval stage, yet it appears that this is passed entirely within the host. In the case of *G. contortulus,* the young second-instar larva assumes a characteristic arched or U-form and begins to force its way out through the thin membrane between two of the anterior abdominal segments. The first exuviae still envelops the dorsum as this takes place. After emergence, the head and anterior third of the body remain buried in the wound, and the posterior portion of the body is bent forward ventrally, the tip lying near the head. At this time, the larva has the appearance of a minute, transparent vesicle.

Three molts take place externally, each skin in turn splitting longitudinally along the mid-dorsal line and remaining adherent, in leaf-like form, to the venter and sides of the larva. These successive skins, of increasing size, make up the larval sac. A gradual darkening of the exuviae takes place until they are shining black, and the third exuviae is distinctly rugosely sculptured.

The break effected in the intersegmental membrane of the host by the second-instar larva is evidently brought about by pressure alone, for the mid-dorsal portion of the parasite body is that which is in direct contact with the membrane. In some species, the young larva appears to be enveloped in a hernia-like distention of the membrane; but this is in reality an unbroken exuviae, and the split along the median dorsal line occurs as the larva increases in size. Fenton states that the larva is at no time exposed to the outside air, for the successive exuviae do not split until there is another beneath. On the basis of the illustrations given, there would seem to be some doubt that the first exuviae of the sac is the actual first exuviae of the larva. The former shows six pairs of spiracles, which is not in accord with the known characters of the sacciform first-instar larva.

During the second to the fourth stages, the head and first thoracic segment of the parasite larva remain embedded in the wound, and in some species a fleshy ventral thoracic process and the pericephalic ring aid in holding this position. The body retains the U- or V-shape, with the posterior end brought forward ventrally almost to the head, until the fourth molt.

There is a considerable variation among species in the color of the larval sac. The first exuviae are always shining black, the second finely sculptured at the outer margins, and the third rugose or punctate. Although the sac is black in most species, yet some are yellow, green, or brown, and in the light-colored forms there is a distinct banded appearance, each band representing a segment. The larva itself is white, and the freshly cast exuviae are colorless and they darken gradually.

The sides of the larva, including the spiracular areas, are covered by the exuviae, which adhere closely, and consequently some adaptation for respiration is necessary. Fenton found that tracheae extend from the first pair of spiracles of the third, or innermost, exuviae of the sac to the corresponding spiracles of the larva, and these may serve as air channels.

The position of the larval sac upon the body of the host is relatively constant within a given species. In the great majority of species, this is between two abdominal segments; some sacs are in the anterior region and others further caudad, and they may be either dorsal or lateroventral. The sac of *Pseudogonatopus stenocrani* Perk. on the nymphs of *Sterocranus*

dorsalis Fitch is found dorsally in an erect position between the wing pads; it has an extraordinary wheel-like appearance, due to the segmental bands on the exuviae. A number of genera form the sac beneath a wing lobe; that of *Neochelogynus* is usually immediately behind the posterior coxa, though in *N. coriaceus* Perk. it is at the side of the neck.

The information regarding the point of oviposition in the host body and that at which the sac later appears indicates that they are identical and that the larva possibly utilizes the weakened point in the integument, caused by the oviposition puncture, in forcing its way out of the body. Attention has been called to this by Fenton in his discussion of *Gonatopus*, of which the larva "pushes its way along the path previously made by the ovipositor toward the external point of insertion of the latter." This is quite probable, for the young larva is evidently incapable of

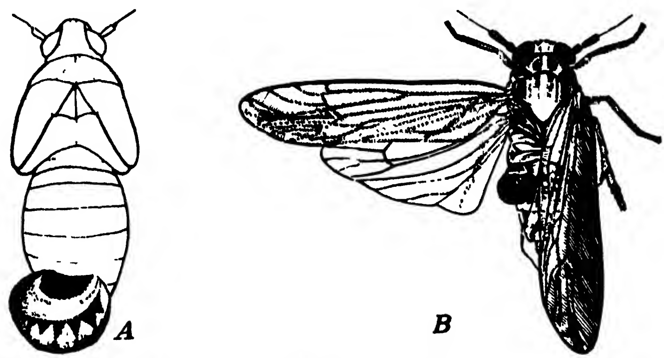


FIG. 149.—Leaf hoppers bearing larval sacs of Dryinidae. *A*, *Haplogonatopus japonicus* E. & H. upon a nymph of *Delphacodes furcifera* Horv. (*from Esaki and Hashimoto*, 1931); *B*, *Pseudogonatopus hospes* Perk. upon an adult *Perkinsiella saccharicida* Kirk. (*from Swezey*, 1936).

locomotion and is not deeply embedded in the tissues. Other authors, however, are not of this opinion; Perkins states that the point of oviposition of *Echthrodelphax* is not constant and yet the sac always appears beneath a wing lobe.

In the genus *Aphelopus* the portion of the body of the parasite larva that is internal is enveloped by a cellular mass of host tissue. This "cyst" was first studied by Keilin and Thompson in *Typhlocyba* adults parasitized by *A. melaleucus*. It first appears about the "embryo" and enlarges as development progresses. The envelope is stated to be formed by a proliferation of the hypodermal cells, and it prevents direct communication between the parasite larva and the body cavity of the host. It persists until the beginning of the last larval stage, and all food materials consumed by the larva are derived from or through it. This cyst is likened in function to a placenta in animals and to a plant gall.

Fenton has observed the cyst in *Erythroneura* parasitized by *A. comesi* Fent. and found that it occupies a large portion of the body cavity and "serves as a means for absorbing, storing up, and then in turn giving up in a modified manner food for the parasite that otherwise would have been utilized by the host." In addition, a layer of hypodermal cells is developed around the wound, which apparently represents an unsuccessful healing effort. In several other genera that were studied, there was no trace of a cyst formation; it may be limited to *Aphelopus*.

The mature larvae of all species are appreciably different from the preceding instars and are capable of considerable movement incident to freeing themselves from the sac or host body and the search for a suitable place for pupation. According to Mik (1882), the larvae of *G. pilosus* Thoms. always move upon their backs; this habit is also mentioned by Fenton. In all species, they leave the body of the host when feeding is complete, and the great majority spin their cocoons in the soil, though a number do so upon the foliage not far distant from the host remains. According to Swezey (1903), *Dryinus ormenidis* Ashm. utilizes the host remains as a covering over the cocoon, and *Neodryinus* spp. use the larval sac for this purpose. *H. americanus* Perk. forms its cocoons upon various objects on the surface of the ground.

The cocoons usually consist of two layers, the inner one being compact and the outer covering rather loosely woven. Cocoons spun upon foliage may be merely an arched covering attached at the margins to the leaf surface.

The manner of development of *A. theliae* is strikingly different from all other Dryinidae in that the entire larval feeding period is passed within the host body, with the consequent complete absence of the external larval sac on parasitized hosts. The death of the host takes place during the penultimate larval stage, and a molt occurs coincidentally with emergence from the host body. Emergence is effected through individual incisions made in the intersegmental areas of the venter of the abdomen. In the sac-forming species, death of the host occurs as a result of the gross feeding of the mature parasite larva, though in some species it may live for a short time after the larva has left the body.

The number of larval instars has been determined with certainty in only a few species, but five is evidently the normal number. The first of these is found within the host body; the following three are external, enveloped in the sac and entirely incapable of movement; and the fifth is an active form which completes feeding and then crawls away for pupation. In *A. theliae*, on the other hand, no feeding takes place after the fourth molt. Fenton implies the occurrence of a sixth instar, inasmuch as he distinguishes between the fifth and the mature larva.

Sex Ratio, Parthenogenesis, and Polyembryony.—Perkins states that "some of the Dryinidae are able to reproduce their kind parthenogenetically, and probably frequently do so in a state of nature." In one species of *Pseudogonatopus* reared from field material, the females predominated in the ratio of 40 to 1, and this was assumed to indicate that unisexual reproduction is normal for the species. *Gonatopus contortulus* consistently produces female progeny from unmated females, and males have not yet been found. Males likewise have not been found or reared in the genera *Eugonatopus* and *Agonatopus*.

In the case of *Aphelopus theliae*, it is assumed by Kornhauser that mated females produce female progeny and virgin females male progeny. All offspring from a single egg are of the same sex, and mixed broods are attributed to duplicate oviposition. This explanation is the one most frequently advanced to explain the mixed broods of the polyembryonic Encyrtidae and Platygasteridae but is an assumption not supported, in this instance, by experimental evidence.

The occurrence of polyembryony in *A. theliae* is of particular interest. This species is the first representative of the Vespoidea known to exhibit this mode of reproduction. Also, the host groups in which it takes place are thus extended to the Membracidae. Although the evidence presented by Kornhauser with respect to the development of the polygerm is not complete, yet the known facts in the biology of *Aphelopus* are all in accord with those which have been fully substantiated in other polyembryonic groups. These may be briefly stated as follows: (1) A single egg is deposited at each insertion of the ovipositor. (2) Forty to sixty larvae develop to maturity in each host. (3) Emergence of the entire brood from the host is simultaneous. (4) The progeny from a single egg are all of the same sex. (5) Pure broods of either sex occur in nature. The growth of the egg into a polygerm mass, then into branching chains of embryos, and finally the breaking up of the chains into separate individuals, each enveloped in a nutritive envelope, were observed.

The Life Cycle.—The time required for the completion of the life cycle has been determined for only a few species. That of *Gonatopus erythrodes* is 35 to 40 days and of *Aphelopus* sp. on *Typhlocyba pomaria* McA. from 50 to 75 days. The period that elapses from oviposition until the appearance of the larva externally is often very short, being only 3 or 4 days in *Pseudogonatopus hospes*, 5 to 7 days in *G. contortulus*, one to three weeks in *Aphelopus typhlocybae* Mues., and up to 25 to 30 days in *Aphelopus* sp., near *microleucus* Perk. in *T. pomaria* McA. There is a correspondingly great variation in the duration of the external feeding phase, which ranges from 4 days in *Aphelopus* sp. to 21 to 27 days in *G. contortulus*, with two or three weeks being the more frequent period. Most species occurring in temperate regions have two generations each year. So

far as known, the hibernation habit in the family is consistent, and only mature larvae or prepupae, in the cocoons, are found during the winter. *A. theliae*, however, is believed to be in the pupal stage during this period.

EFFECT OF PARASITISM UPON THE HOST

The effect of dryinid parasitism upon the sexual characters of the host has attracted a great deal of attention in those species which are mature before death. This subject was first discussed by Giard (1889) in the case of *Typhlocyba* spp. parasitized by *Aphelopus melaleucus*. In both sexes, the reproductive organs were reduced in size and modified in form. He characterizes the effect upon the host as "parasitic castration." Kornhauser, in his extended study of the effect of parasitism by *A. theliae* upon *Thelia bimaculata*, found that many alterations in external form take place. Male adults assume either partly or completely many of the sexual characteristics of the female, and the degree of change depends upon the stage of development of the parasites during the fifth nymphal instar of the host. The changes are most pronounced in the individuals in which oviposition has taken place in an early instar. The most striking changes in the male are the assumption of the pigmentation of the female and an increase in size approaching that of the latter. Various sclerites associated with the genital appendages show a considerable modification toward the opposite sex; but the appendages themselves are not changed, but merely reduced in size, and lose their specific characteristics. The females show no change in pigmentation or size but undergo a similar reduction in sex organs. None of the changes noted was due to a retention of nymphal characteristics. Parasitism generally causes the degeneration of the gonads, resulting in partial or complete "castration" in both sexes. It also brings about a marked accumulation of fat in the abdomen of the host.

In certain Cicadellidae and Fulgoridae parasitized by *Gonatopus*, *Haplogonatopus*, and *Chelogynus*, it was found by Fenton that parasitization of adult females does not result in immediate cessation of reproduction, though interference with this function is very soon evident and complete inhibition follows.

The species that develop externally, and these comprise all that have been studied except *A. theliae*, inhibit molting of the host after parasitization, or at least after the external larval phase is assumed.

IMMATURE STAGES

The egg and early larval instars of the family have been described for only a very few species, and for these inadequately. The egg of *Gonatopus erythrodes*, as described by Fenton, is 0.2 mm. long, 0.12 mm. wide, oval in outline, without sculpturing, and pale yellow in color. That of an undetermined species of the same genus is somewhat similar, though kidney-shaped. In *G. contortulus*, the egg is dark-gray in color.

Kornhauser describes the egg of *Aphelopus theliae* as oval in form and 0.145 mm. in length. At oviposition, this egg is accompanied by several spheres, 0.025 to 0.035 mm. in diameter, each covered with a chitinous shell, which contain yolk-like material. It is stated that these spheres, of unknown function, "are developed in the female *Aphelopus* from single cells in a sac-like pocket ventral to and leading into the posterior portion of the oviduct, just below the opening of the spermatheca."

The first-instar larva of *A. theliae* is sacciform, or embryonic, in type, with no distinguishable organs, and the mouth parts are not sclerotized. The embryo of *A. melaleucus* mentioned by Keilin and Thompson is probably the first instar.

The second-instar larvae of all species which develop externally are strongly curved as a result of being enclosed within the first exuviae. That of *A. comesi* is distinguished by the possession of a pair of bulbous lobes on the cephalic region, which are considered to be the mouth parts, and by the presence of nine pairs of spiracles. The second instar of *A. melaleucus* (Fig. 150*D*) is identical in general characters, and the cephalic lobes are designated as the mandibles. This larva also bears a heavily sclerotized pericephalic ring. It may, in reality, be a later instar, for only three are mentioned.

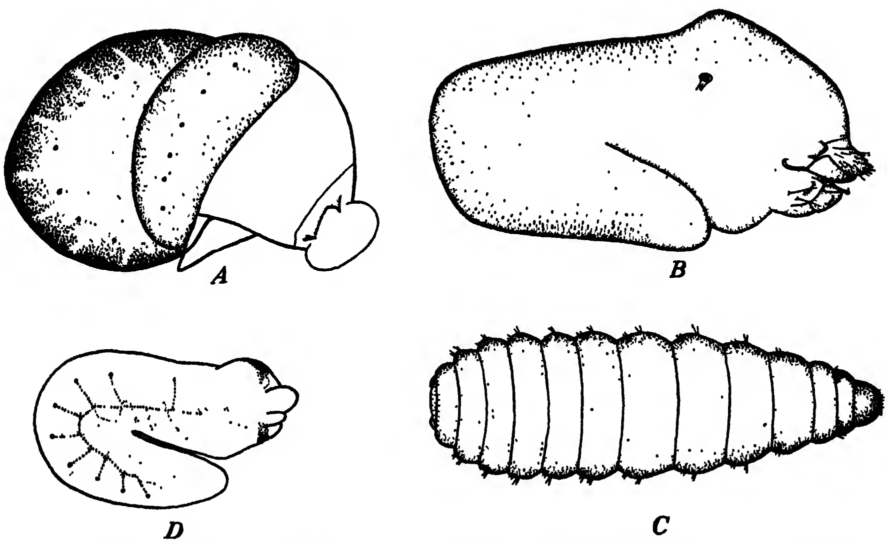


FIG. 150.—Immature stages of the Dryinidae, *A*, the third-instar larva of *Gonatopus contortulus* Patt., showing the larval sac; *B*, fifth-instar larva of same, removed from the sac; *C*, mature larva of *Gonatopus* sp. (*from Fenton*, 1918); *D*, second-instar larva of *Aphelopus melaleucus* Dalm., removed from the sac (*from Keilin and Thompson*, 1915).

The third-instar larva of *G. contortulus* (Fig. 150*A*) and certain other species is distinguished principally by a fleshy cone-shaped process situated ventrally immediately behind the head. The mandibles are very large and fleshy, and the pericephalic ring bears two pairs of spine-like projections. There are still nine pairs of spiracles.

The fourth-instar larva shows the fleshy head lobes assuming somewhat the form of mandibles. The penultimate larval instar of *G. contortulus* (Fig. 150*B*), which is described as the fifth, is very robust in form and has the mesothoracic spiracles very large whereas the remaining eight pairs are small and indistinct. In *A. theliae*, as in other species of the genus, the pericephalic ring persists in the fourth instar; this larva,

because of its prominent mouth parts, has been termed "megagnathic" by Kornhauser.

The mature larvae are usually white in color, occasionally pink or green, of the normal hymenopterous form, and distinctly segmented (Fig. 150*C*). Those of the genus *Aphelopus* bear many integumentary spines and setae, which may be arranged in distinct segmental bands on the dorsum and sides, as in *A. theliae*. In the Dryininae, these spines and setae are largely lacking. The mandibles are usually heavy and curved and may be either simple or denticulate. There are 10 pairs of spiracles, of which the mesothoracic pair is much the largest. In *Dryinus pyrillae*, there are only 9 pairs, situated on the first and third thoracic and the first seven abdominal segments.

RHOPALOSOMIDAE

This is an aberrant family, consisting of a very few genera and species, that has been variously placed systematically. The only information available regarding their habits and immature forms is that presented by Hood (1913) on *Rhopalosoma poeyi* Cress. A single adult female of the jumping tree cricket, *Orocharis saltator* Uhler, was found to bear a parasitic larva attached externally to the side of the abdomen. This larva was reared to maturity and proved to be of the above species. The death of the host occurred concurrently with the attainment of larval maturity.

The mature larva is very robust, measuring only twice as long as wide. The successive cast skins remain as a pad beneath the body, much after the manner of *Tiphia*, and those carried by the above individual indicated at least five larval instars. Each had apparently 10 pairs of spiracles, the exact position of which is not given.

EUMENIDAE

The members of this family are solitary in habit and exhibit a great variety in the location and in the manner of forming the cell to receive the prey. Some build vase-like or spherical cells of sand, mud, clay, or masticated leaf tissue that are fastened to twigs or other objects; others utilize tubular cavities in stems and partition off each successive cell; finally, a number of species make burrows in the soil, and a few utilize the abandoned cells of other wasps.

The great majority of species provision the nest with lepidopterous larvae, though some are known to utilize larvae of Tenthredinidae and Chrysomelidae. The family is consequently entirely beneficial. Each cell is provided with a number of permanently paralyzed larvae, and the egg is deposited just before the cell is closed. Roubaud (1910) has given an excellent account of several species of *Synagris*, which exhibit interesting departures from the normal habits of the family. The female of *S. cornuta* L. places the egg in the cell as soon as it is completed, and no provisions are brought in until after hatching has taken place. No

caterpillars are ever brought to the nest, but the parent female feeds the larva periodically with chewed-up bits of the body contents of freshly killed victims. In *S. sicheliana* Sauss., the caterpillars are placed in the cell at necessary intervals, and it is closed when the larva is about three-fourths mature. The same general habit of maternal care is recorded in several related genera.

The eggs are usually somewhat elongate and bear a stalk at one end which in some species is longer than the egg body and by means of which it may be suspended from the wall of the cell. The newly hatched larva may retain its attachment to the eggshell for a period after hatching.

The hunting habits of *Odynerus herrichi* Sauss. (Spooner, 1934) are of particular interest. The female searches out the tortricid larva, upon which it preys, in its web, bites a hole in the top, and then thrusts its sting through the web. As a result of this disturbance, the caterpillar emerges through the hole and drops to the ground. The wasp thereupon drops perpendicularly to the ground, also, captures the caterpillar, and carries it to the nest. If the caterpillar is not found at the first attempt, the wasp returns to the plant, finds the hole in the web, and again drops to the ground to renew the search.

VESPIDAE

This family includes the papermaking wasps, which often live in large colonies consisting of a queen, males, and workers. In general, they feed the brood with masticated portions of animal matter and at times with fruit juices, nectar, and honeydew, also. The animal food consists mainly of the body contents of caterpillars and other soft-bodied insects. It is because of this habit that the family is of some importance in the natural control of injurious insects, particularly the exposed foliage-feeders.

The so-called "Spanish Jack," a species of *Polistes*, is given credit for markedly reducing the population of several pests in certain islands of the West Indies and has been intentionally colonized on several islands. Bartlett (1938) mentions that several species of Vespidae, the most numerous of which is *P. crinitus* var. *americanus* F., are largely responsible for holding *Laphygma frugiperda* S. & A. in check in Puerto Rico. R. B. Friend observed the females of *P. pallipes* Lep. cutting open the leaf mines of the birch leaf miner, *Fenusa pumila* Klug., and feeding upon the larvae. Not all the activities of the different species of *Polistes* are beneficial, however, for the food range is sufficiently wide to include various insects that are themselves beneficial. An instance of this is the extensive attack of *P. orientalis* F. upon honeybees in Egypt.

Stenogaster spp. in the Philippine Islands feed their young with a milky-white jelly which is made up from the chewed-up bodies of tiny midges taken from spider webs (Williams, 1928).

According to Wheeler and Taylor (1921), *Vespa arctica* Roh. is a permanent social parasite in the nest of *V. diabolica* Sauss., and her brood is reared by the workers of the latter.

SPHECOIDEA

The members of this superfamily of fossorial wasps very largely provision their nests with other insects. As a whole, the group may be regarded as beneficial, the number of pest species that are preyed upon far exceeding that of the entomophagous species. The habits of the group are much simplified as compared with the Vespoidea and Apoidea, and there is little development of a complex social life such as is found in the latter superfamilies. The nests, comprising either one cell or a group, are found in diverse places. The majority of species burrow in the soil; but some build nests of clay, mud, or sand, and others nest in stems of plants or in a great variety of cavities of suitable size.

The range of host preferences is exceedingly wide, including practically all the more common orders, though the most common groups preyed upon are the Orthoptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Diptera, and finally, the spiders. With many species, particularly those attacking large hosts, only a single victim is placed in each cell, whereas others may require a considerable number to bring each larva to maturity. The prey may be temporarily or permanently paralyzed, or it may be killed by the sting.

Only a brief account will be given of the habits of the families of this group. For more detailed information, the reader is referred to the extended publications of J. H. Fabre, C. Ferton, G. Grandi, R. Grandori, Sir John Lubbock, H. Maneval, G. W. and E. G. Peckham, P. and N. Rau, E. Raboud, and F. X. Williams.

AMPULICIDAE

The family comprises only a small number of species, and relatively little is known regarding their host preferences and habits. They seldom dig burrows but utilize natural cavities for nests, and the comparatively few species that have been observed provision them with immature cockroaches. An interesting description of the habits of *Dolichurus stantoni* Ashm., which attacks the nymphs of several genera, is given by Williams (1919*b*). These cockroaches are very agile, and when one is located by the female it is first grasped by a cercus or leg, following which the sting is inserted in the throat or thoracic region. It is only partly paralyzed, however, and is still capable of slow movement. The

wasp now grasps an antenna near the base and leads or drags the victim to the nest (Fig. 151). After it is put in the desired place, the female deposits her egg somewhat obliquely upon one of the middle coxae. The egg hatches in one or two days, and the larval feeding period is completed in only four or five days. This species was introduced into Hawaii from the Philippine Islands in 1917 and has become well-established.

Ampulex caniculatus Say (Williams, 1929) has a similar habit and attacks principally *Poreoblatta virginica* Bam. Paralysis of the cockroach is complete, and the female then bites off the distal three-fourths of the antennae and feeds upon the body fluids exuding from the wound before transporting the prey to the nest. The roach recovers quickly, but only partly, from the effects of the sting and is then led to the nest, after which the egg is deposited upon the coxa of one of the middle legs. No other species of the family is known to amputate the antennae of its host.

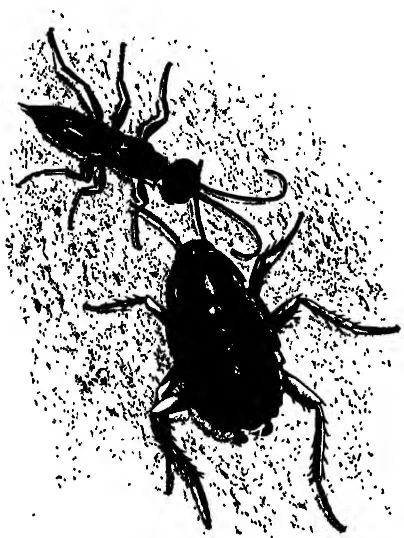


Fig. 151.—A female of *Dolichurus stantoni* Ashm. dragging a young cockroach to her burrow. (*From Williams,* 1919.)

Hingston (1925) gives an interesting account of the attack of *A. assimilis* Kohl upon a cockroach, *Shelfordella tartara* Sauss., in India. Only females hosts are attacked, inasmuch as they are wingless and consequently cannot escape so readily. Paralysis is not complete, but the sting quiets the roach sufficiently so that it can be led to the burrow, which is usually that of a beetle in a palm tree. The search for a suitable site for storage of the prey takes place after the latter has been found and stung, rather than before, as in the species already discussed. The egg is fastened to the femur of one of the legs. Initial feeding takes place at a puncture in the femur, and it is stated that the partly grown larva enters the body of the roach and feeds for a time as an internal parasite, the thoracic tissues being consumed first. The body contents, but not the exoskeleton, are eaten and the cocoon is spun within the abdomen of the host.

SPHECIDAE

This family comprises a large number of species, the majority of which make their nests in the soil, though some form them in hollow stems or

build mud cells upon foliage or elsewhere. A given species may limit itself almost to a single host species, whereas others may utilize members of several related families. The variety among the prey is considerable, ranging from spiders to locusts, grasshoppers, mole crickets, cockroaches, and lepidopterous larvae. Among the better known genera, *Sceliphron* and *Chalybion* store their nests with spiders; *C. cyaneum* Dahlb. of North America utilizes the notorious black widow spider. *Podium*, *Chlorion*, and *Trigonaspis* prey upon a variety of Orthoptera; some species of *Sphex* attack the larger Orthoptera, principally grasshoppers; others of the genus store their nests with lepidopterous larvae.

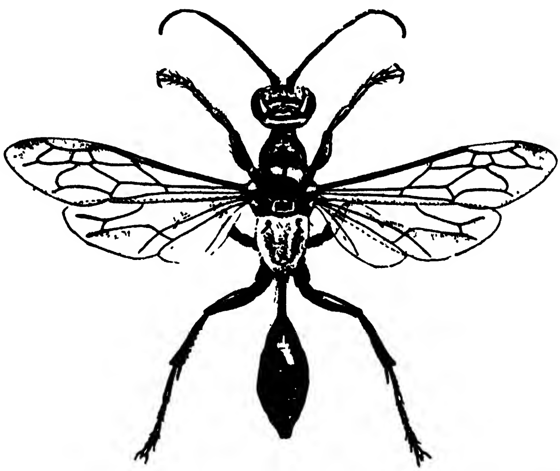


FIG. 152.—The adult female of *Podium flavipenne* Latr. (*From Williams*, 1928.)

C. B. Williams (1933) mentions the attacks of *Sphex aegypticus* Lep. upon migrating swarms of the desert locust in East Africa. During one season, vast numbers of females followed the locust migration, and enormous numbers of stored nests and paralyzed locusts were left behind as the swarm moved on. This wasp had not previously been seen in the particular section in which the observations were made. It is stated that in spite of the very extensive nest-making that took place the brood did not develop and no emergence of adults occurred. It was noted that no males accompanied the migration; thus, lack of fertilization may possibly explain the complete mortality that occurred.

S. nigellus Smith stores its nests with adults or nymphs of *Conocephalus*, etc. (Piel, 1933*b*). The nesting habit is quite different from that of the species mentioned above, as the prey is stored in cells formed in hollow stems of bamboo. The victims are completely paralyzed and the legs and antennae amputated before being stored. In spite of this drastic treatment, they remain alive for five or six days. After

the series of cells is provisioned, the end of the bamboo stem is closed with a bundle of grass blades or stems, which may project conspicuously from the opening.

S. lobatus F. of tropical Asia develops upon the cricket, *Brachytrypes portentosus* Licht. (Hingston, 1925, '26); it is apparently specific in its choice of prey. The female wasp searches out the host cell in the soil, drives out the occupant, and then pursues and captures it above ground. A protracted battle usually ensues; but finally the parasite is able to grasp one of the wings with her mandibles, and the sting is then inserted in the thoracic region and finally in the neck. After effecting complete, though only temporary, paralyzation, the wasp drags the cricket by its antennae back to the burrow from which it came. This is one of the few species of the family that makes no burrow or cell of its own.

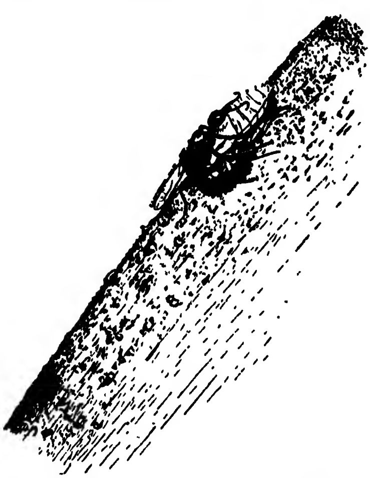


Fig. 153.—A female of *Podium haematogastrum* Spin. ovipositing upon a young cockroach near the entrance to her burrow on the side of a termite mound. (*From Williams*, 1928.)

Observations have been recorded on several species of *Sphex* that store their nests with caterpillars. *S. hirsuta* Scop. (Bougy, 1935) utilizes noctuid larvae. The latter are nocturnal in habit and during the day are found in the soil at the bases of their food plants. The female wasps search out the larger caterpillars in the soil and sting them into complete and permanent paralysis, first in the thoracic region and finally in the posterior segments bearing the false feet. While the caterpillar is being dragged to the burrow, its thorax is grasped between the mandibles and its body drags behind, the venter being uppermost. The egg is usually placed somewhat dorsally on the anterior portion of the abdomen. The larva, when partly grown, may enter the body of the caterpillar to complete its feeding.

In the southwestern United States, *Prionyx atratum* Lep. is known as a hunter of nymphs of grasshoppers. The female stings a number of victims at one time but uses only the last one in provisioning the nest. This habit increases the value of the wasp in grasshopper control.

Williams (1928) has studied several South American species of the genus *Podium*, which store their nests with young and occasionally adult cockroaches of the genus *Epilampra*. The females have the unusual habit of depositing the egg upon the victim just prior to dragging it into the burrow, in contrast to the general habit of the family of ovipositing

after the nest is fully provisioned. As in the case of most other members of the family that attack Orthoptera, the egg is placed at the base of one of the coxae. The nests are built in hard ground that is free from vegetation, and *P. haematogastrum* Spin. may even be found nesting quite frequently upon the sides of termite mounds.

The effect of the sting of the female Sphecidae upon the host ranges from only temporary to permanent paralysis and, in some species, to immediate death. Crickets stored by *S. lobatus* recover almost completely in 10 to 15 minutes; yet apparently a considerable lethargy follows, for they show no inclination to escape from the burrow. Noctuid larvae stung by *S. hirsuta* live a maximum of 39 days. In a number of species that attack caterpillars, the female malaxates the venter of the victim after it has been stung. Some species pinch the neck extensively and feed upon the fluids that exude from the mouth.

CRABRONIDAE

This family comprises a large number of species of small size that build their nests in hollow stems, abandoned galleries in wood, or burrows in the soil. The galleries in wood are usually of coleopterous borers, and they may be further elaborated by the new occupant to provide cells for the reception of the brood. The nests are of two types, one being linear and consisting of a row of cells, the second having lateral galleries branching off from the main tunnel. The prey utilized in provisioning the cells is exceedingly varied and ranges from spiders and mites to adult Diptera, Homoptera, Coleoptera, Hymenoptera, Lepidoptera, and Ephemerida, with the Diptera predominating. Manifestly, the group is not entirely beneficial, in view of attack upon spiders and certain parasitic and predaceous Diptera and Hymenoptera. Syrphid flies are quite frequently attacked, and the European *Lindenius pygmaeus* Rossi provisions its cells with parasitic chalcidoid wasps of the genus *Pteromalus*. There appears to be little consistency in the selection of prey by the various groups in the family; the species of a single genus may utilize Diptera, Coleoptera, or Hymenoptera. A single species may even limit itself to only one sex of the insect attacked, whereas the opposite extreme is represented by those species which prey upon several orders. Hamm and Richards (1926) give an account of the prey and nesting habits of a number of species occurring in England.

The cell situated farthest from the nest entrance is provisioned first, and the egg is usually deposited upon the first victim placed in each cell. This is not an invariable rule, however, for *Crabro brevis* Lind. oviposits only after the full complement of beetles has been placed in the cell.

The members of the genus *Oxybelus* are relatively small wasps that make their burrows in sandy places and provision the cells with flies.

O. quadrinotatus Say, which has been studied by the Peckhams (1898), carries her prey in an inverted position beneath the body, the head grasped by the hind pair of legs in such a position that the entire abdomen projects caudad beyond her body. The flies are killed at the time of capture, though how this is accomplished is uncertain. In the case of other species, it has been stated that death ensues as a result of the crushing of the thorax with the mandibles. The specimens of the above species were intact, however, when brought to the nest.

Hypocrabro stirpicola Pack., which has also been studied by the Peckhams, has the very unusual habit of continuing its activities during the night. The flies used in provisioning the nest are of the families Anthomyiidae and Calliphoridae, which are dead at the time they are stored. *Xestocrabro sayi* Ckll. (*sexmaculata* S. & F.) does not harm its prey in any way; when the cells are opened, the flies and gnats are quite active and some are able to fly away.

Crabro brevis Lind. (Grandi, 1925) stores its nests with adult chrysomelid beetles of the subfamily Halticinae. Those found in a cell may represent several species or even genera, and in different localities the wasp may specialize upon different species. The nest comprises 6 to 10 cells, and each of these is provisioned with 12 to 25 beetles. Various species of the genus are reported to carry the prey impaled upon the sting.

A European species, *Ceratocolus alatus* Panz., stores its nests with adult moths of *Phlyctaenodes sticticalis* L., and the cocoons are made up largely from the wings of the prey. This habit of incorporating the remains of the victims in the cocoon is common to many species.

Tracheloides hicksi Sandh. is reported to attack ant columns on tree trunks, the female seizing an individual and flying away with it to a near-by branch, where it is then stung.

TRYPOXYLONIDAE

The nests of this family are often composed of a considerable number of mud cells, arranged frequently in tubular form on a solid surface. Each aggregation may comprise the cells of a number of successive generations. Other species utilize crevices or holes in stems, walls, etc., or they may burrow in the soil. With few exceptions, they provision their cells with spiders.

Trypoxylon rubrocinctum Peck. and *T. albopilosum* Fox have been studied in some detail by the Peckhams (1895, '98). The females of these species utilize existing burrows in woodwork or masonry that have been abandoned by the makers. The first-named species provisions its cells with 7 to 12 spiders, whereas the second, being larger, requires 25 to 30. The victims represent many genera and even families, though

usually the majority belong to the Epeiridae. The egg is laid upon the side or dorsum of the abdomen of the last spider placed in the cell.

LARRIDAE

The members of this family prey very largely upon Orthoptera and Hemiptera. The species of the genus *Larra* are true parasites of the mole crickets and in most cases permit them to continue an active life after the egg is laid. Other genera, however, are diggers and store the prey in underground cells. The species of *Notogonidea*, *Liris*, and *Tachytes* mainly attack crickets; other genera prey upon Locustidae and Mantidae, and a few upon Hemiptera, Hymenoptera, and Psocidae.

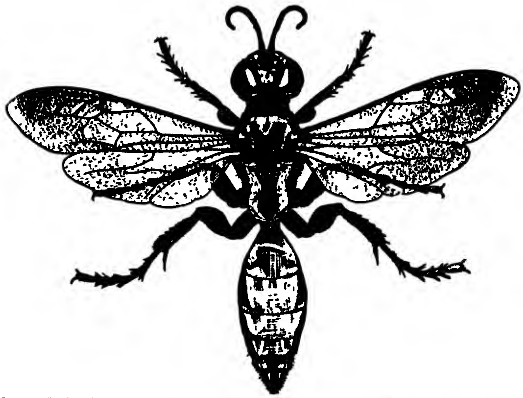


FIG. 154.—The adult female of *Larra americana* Sauss. (*From Williams*, 1928.)

Several attempts have been made to utilize species of Larridae in biological control of insect pests. *Larra luzonensis* Roh. was imported into Hawaii from the Philippine Islands in 1921 and 1925 and *N. subtesselata* Smith in 1921, the former against mole crickets and the latter against field crickets. Both of them became established. More recently (1936 to 1938), *L. americana* Sauss. of Brazil has been successfully colonized against the "changa," *Scapteriscus vicinus* Scudd., in Puerto Rico.

An extended account of the habits of *L. analis* F. is given by C. E. Smith (1935). This species attacks the mole cricket, *Gryllotalpa hexadactyla* Perty, in the southern sections of North America. The female makes an extended search for her victims, driving them out of their soil burrows, and immobilizes them by an initial sting at the juncture of the thorax and abdomen. Complete paralysis is brought about by further stinging in the neck. The female feeds upon the body fluids through a puncture made at the base of one of the forelegs. She then takes up a position on the venter of the host body, with the head directed caudad, and rasps the surface of the host body just behind the last pair of legs with the tip of the abdomen; it is at this point that the egg is deposited.

The host is then abandoned on the surface of the soil. It recovers from the effects of the sting in 5 to 10 minutes and resumes its normal activities. The female parasite appears to make a determined effort to eliminate any eggs or larvae that may already be present upon the body of the host. The general area of oviposition is first gone over with the tip of the ovipositor; if any obstruction is encountered, such as an egg or young larva, the female parasite turns about and dislodges it with the mandibles.

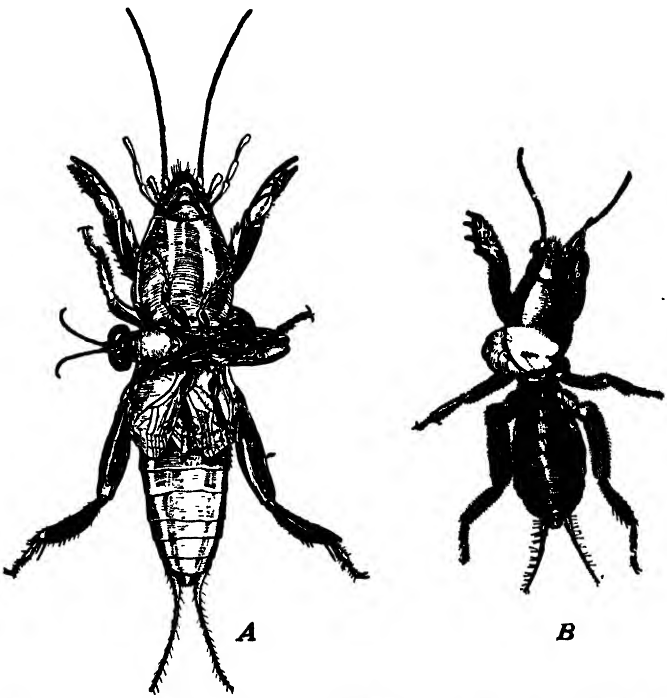


FIG. 155.—Larrid parasites of mole crickets. *A*, a female of *Larra scelesta* Turn. attacking *Gryllotalpa nitidula* Serv.; *B*, a larva of *L. carbonaria* Sm. feeding upon a nymph of *G. hirsuta* Burm. (*From Williams*, 1928.)

The host may be of any stage beyond one-third grown when attacked. At hatching, the first-instar larva punctures the host integument immediately beneath the egg, and through the chorion; but both the head and posterior end of the body remain shielded within the shell throughout the stage. The head of the second-instar larva remains enveloped in the first exuviae; and the successive instars to the fifth have the posterior portion of the body, and the venter, encased in the exuviae. From the third molt onward, the head is embedded in the wound.

The egg stage of the parasite covers four days. The host, irrespective of its size, is always killed just prior to the fourth larval molt of the para-

site, this being about eight days after hatching. It dies in its burrow in the soil, and the fifth-instar parasite larva then completes its feeding and spins the cocoon. The cycle from egg to adult covers about seven weeks under summer conditions, of which five weeks are passed in the cocoon.

Williams (1919*b*, '28) has made extended studies on the habits of a number of species of Larridae occurring in the Philippine Islands, Australia, and South America. All species of *Larra* were found to paralyze the host only temporarily and to abandon it on the surface of the ground after oviposition. In the case of many species, there is an extensive malaxation of the host body prior to deposition of the egg. The position of the egg on the host body varies somewhat. The eggs of all species studied by Williams are placed transversely and ventrally between the first and second pair of legs, in contrast to the position of the egg of *L. analis*, but they differ in relation to the median line and the lateral margin of the host. The anterior pole is directed toward the lateral margin of the thorax. An undetermined species of the genus observed in Ecuador is distinguished biologically by the habit of placing its egg perpendicularly on the thorax above the base of one of the hind legs, with the anterior pole outward. The egg of *L. scelesta* Turn. is exceptionally small, measuring only 1.7 mm. in length; this reduction in size may have developed as a consequence of the activity of the hosts. Species having larger eggs paralyze the host more completely, and there is consequently less danger of injury.

The life cycles of all of these species are relatively short, covering only one month or slightly longer. The egg stage of *L. femorata* in Australia is prolonged to seven and one-half days.

Liris haemorrhoidalis magnifica Kohl, which attacks crickets of the genus *Gryllus* in Australia, has also been studied by Williams. This species builds its nest in the ground, and the burrow is 1 to 2 m. in depth. The host is temporarily paralyzed and dragged by the antennae into the nest, and the egg is then placed ventrally on the thorax between the first and second pairs of legs. Several crickets may be placed in each cell. Each burrow may comprise a number of cells and require several weeks for provisioning. A tendency toward social life is revealed in this species, for several females may utilize the same burrow. The egg of *L. magnifica* is of exceptional size, measuring 4.0 mm. in length.

Observations have been recorded upon several species of *Notogonidea*, which provision their nests with Gryllidae. The burrows are very short as compared with those of *Larra* and *Liris*, being only 5 to 12 cm. in depth, and they may terminate in only a single cell or in several. Paralysis of the hosts is only temporary; after being placed in the cell, they revive to a considerable extent and are able to walk about but make no

effort to escape. Several crickets are stored in each cell, and the egg is placed on the venter of the thorax of one victim.

Tachytes mergus Fox, a South American species studied by Williams, stores its single-celled nest with several *Tridactylus apicalis* Say. Its manner of capturing and transporting its prey is distinctive. The female wasp has exceptional powers of leaping and may pounce upon the cricket while the latter is in flight, and it is then transported through the air to the nest, rather than dragged along the ground.

Palarus saishiuensis Okam. of Chosen (Korea) stores its underground nest (Fig. 156) with various adult bees and wasps, about two-thirds of

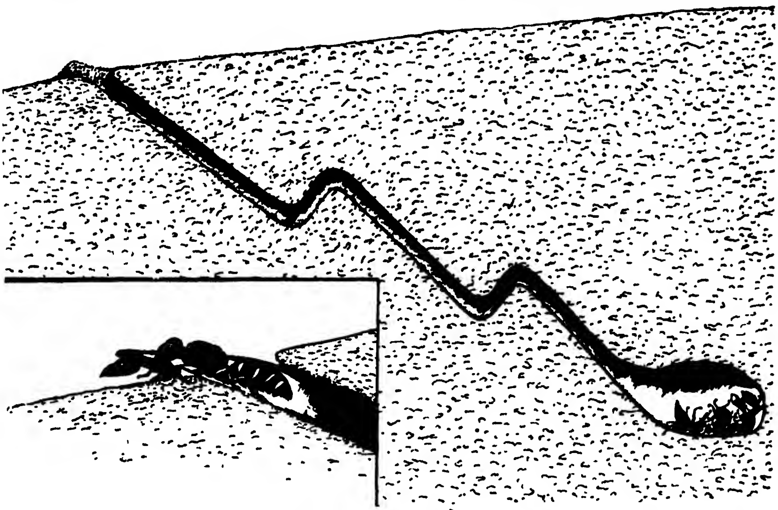


FIG. 156.—The burrow of *Palarus saishiuensis* Okam., showing the rearing chamber at the bottom and (inset) a female dragging her prey into the burrow. (*From Clausen et al*, 1932.)

which are *Tiphia* spp. and the remainder principally Apidae (Clausen *et al.*, 1932). The maximum number of *Tiphia* found in a single cell is 14, though usually the number is much less, and the greater portion of those captured have been found to be females.

P. orientalis Kohl is recorded by Cherian and Mahadevan (1937) as a serious enemy of honeybees in certain sections of India. The female *Palarus* frequents the vicinity of the hives, often perching upon the entrance platform, and pounces upon incoming or outgoing bees, which are stung to complete immobility or killed and are then transported to the nest. The burrow contains three or four apartments separated by 8 to 10 cm., and two to six bees are placed in each. The egg is placed between the head and thorax of one of the victims. Hatching takes place two days later, and larval feeding is complete in five days. Under field conditions, *Palarus* females are each capable of storing 15 to 20 bees

per day, and where they are abundant the depletion of the hive population is considerable. *P. flavipes* F., of Europe and Asia, is also stated to store its nest with honeybees (Ahrens, 1925).

PEMPHREDONIDAE

These relatively small wasps make galleries in twigs or wood, at times utilizing the abandoned galleries of wood-boring insects, and store the brood cells with aphids, though some species prey upon other Homoptera of corresponding size. The Peckhams (1898) have observed the nesting habit of *Stigmus americanus* Pack., which adopts and enlarges old burrows in decaying wood. Several individuals may utilize the same gallery, though they nest separately. Each cell, when complete, contains about two dozen dead aphids, mixed with grains of pith, and the egg is borne upon the body of one of them.

NYSSONIDAE

The family is represented by a relatively small number of genera and species. So far as known, their prey consists mainly of Homoptera, particularly of the families Cercopidae and Membracidae. *Gorytes costalis* Cress. utilizes the adults of several genera, and each of the several cells in the nest in the soil is provisioned with three to six tree hoppers. These are permanently paralyzed and die within one week, which normally covers the period elapsing between deposition of the wasp egg and completion of feeding by the larva. *G. brasiliensis* Shuck. of South America is of similar habit but provisions its nest with various Fulgoridae.

MELLINIDAE

Relatively little is known regarding the habits of this small family. Several species are known to make their burrows in sandy locations and to provision them with adult Diptera.

PHILANTHIDAE

The species of this family are burrowers in the soil, where they excavate a series of cells and store them with adult hosts. The dominant genus *Philanthus* is well-known and preys upon various Hymenoptera, particularly Apoidea.

The depredations of the so-called "bee wolf," *Philanthus triangulum* F. (*apivorus* Latr.), are of special interest and concern to honey producers of some sections of Europe. Fabre (1891) gives an extended account of the habits of this insect in its relation to honeybees. The female *Philanthus* kills the adult bee by stinging it in the throat. She then begins an extensive malaxation of the throat by means of which the honey in the crop is forced up to the mouth, where it is greedily consumed. Alternate malaxation and feeding often continue for an hour or more.

After this is completed, the victim is dragged to the burrow. This extends 1 m. or more into the soil and terminates in a group of cells, in one of which the bee is placed; the egg is then deposited ventrally upon the thorax. It is stated that the larvae are unable to develop to maturity upon bees which have not first been deprived of their burden of honey. A considerably larger number of bees is killed than can be utilized in stocking the nest.

Thiem (1935) gives an extended account of the status of this pest in certain honey-producing sections of Germany. In one locality, nearly two million bees, representing 48 hives, were destroyed in one season. The following season, 31,000 *Philanthus* adults were killed by boys employed for the purpose, and yet it was estimated that one-half million emerged later. The factory and mine dumps of brown coal and salt waste in these areas apparently provide exceptionally favorable conditions for the development of the pest. The only practicable means of control appears to be the elimination of these favored breeding places. In some places, this can be accomplished by covering the areas with soil and inducing a growth of grass. Other measures, practically all of which involve individual treatment of the burrows, are necessary in sandy areas.

P. gibbosus Fab. kills its prey, which consists of adult Halictidae, at the time of capture, and considerable putrefaction takes place before larval feeding is complete (Reinhard, 1924). The burrows may be several meters in length, and they comprise a number of cells. From 8 to 16 bees are placed in each cell, and the egg is deposited upon the last of the series to be brought in, usually a small individual.

A high degree of specialization is exhibited in the attack of *Aphilanthops frigidus* Smith upon ants of the genus *Formica* (Wheeler, 1913). Only the queen ant is attacked, and capture takes place only during the nuptial flight. The wasp responds only to the visual stimulus of the winged individuals and ignores those lacking wings. After stinging of the queen is complete, the wings are cut off and the body is dragged into the burrow. The egg is laid upon an isolated ant which has been cut into two parts, and others are taken from storage and fed to the larva as required. Owing to the fact that flights of any single ant species occur during only a short period, the wasp preys upon a series of species during the season.

PSENIDAE

The members of this small family provision their nests with Homoptera. Barth (1907) has given an account of the habits of *Psen barthi* Vier., which provisions its nest with adult leaf hoppers. When being transported to the nest these are grasped by the neck or thorax with the middle legs and held with the venter or side uppermost. The

nest, which is situated in an old log, comprises a small number of cells, in each of which three to five leaf hoppers are placed. These hoppers apparently are killed by the sting at the time of capture. The egg is attached to the thorax of one of the hoppers in the cell. Similar habits have been recorded by Williams (1919*c*) for *Nesomimesa hawaiiensis* Perk. *P. pallidipes* Panz. (*atratus* Panz.) stores its nests with aphids, which are completely paralyzed; 25 to 30 are placed in each cell. Nest building begins in May and continues without interruption until the end of the season.

STIZIDAE

The members of the family, which number relatively few species, prey upon Orthoptera and Homoptera.

One of the most interesting and common members of the family is the large cicada killer, *Sphecius speciosus* Drury (Riley, 1892) of North America, which stores its nests with adults of the periodical cicada, *Magicicada septendecim* L. The wasps appear in the field in July and August. The cicada is stung to complete paralysis; but it is stated that such individuals will, under proper conditions, persist in good physical condition for more than one year. The victim is of such large size that the wasp experiences difficulty in transporting it to the nest. She accordingly adopts a very ingenious expedient whereby she drags it to some height in a tree and then glides with it as far as possible toward the nest. This procedure may be repeated several times. Occasionally, two cicadas are placed in a single cell, though usually only one. The egg is deposited at one side of the venter of the thorax. Hatching occurs in two or three days, and larval feeding is completed in one week. The cocoon is spun in the cell in the soil and is distinguished by the possession of two irregular rows of "pores" at one side which are considered to serve for ventilation.

Hartzell (1935) has made a study of the effect of the sting of *Sphecius* upon the cicada and finds that lesions are formed in the main parts of the central nervous system similar to those produced by certain chemicals, such as the pyrethrins.

CERCERIDAE

This family, included by some authors in the Philanthidae, is of general distribution; the species of which the habits are known mostly burrow in the soil, often to a considerable depth, and store their nests with adult beetles or andrenid bees. The widespread genus *Cerceris* preys principally upon the coleopterous family Curculionidae.

Fabre (1879), in his study of *Cerceris tuberculata* Vill., found that the weevils stored in the nest were, with very few exceptions, of a single species, *Cleonus ophthalmicus* Rossi. This limitation is apparently

correlated with size; for the *Cerceris* is the largest species known in the section where it was studied, and the weevil species is likewise the largest of the family available. The beetles are nearly twice as large by weight as the wasps that prey upon them. In contrast to this limitation in hosts, the prey of *C. arenaria* L. and *C. ferreri* Lind. comprise a number of genera.

C. clypeata Dahlb., which has been studied by the Peckhams (1898), preys upon *Balaninus*, and these weevils are killed by the sting before being stored. *C. deserta* Say utilizes *Conotrachelus posticatus* Boh., of which a considerable number are placed in each cell. With this species, also, the beetles are either dead at the time of storing or die very soon thereafter.

Williams found that the Philippine *Cerceris angularis* Ckll. stores its nests mainly with long-horned beetles and that *C. spiniger* Roh. shows a preference for Chrysomelidae. In both species, the contents of the cells at times comprise representatives of several families. The egg is attached longitudinally to the venter of one of the beetles.

The victims of *Cerceris* are usually stung in the throat and while being carried to the nest are grasped by the neck or thorax with the mandibles only. P. Marchal mentions the extensive malaxation of the throat of bees of the genus *Halictus* by *C. rybiensis* L. (*ornata* Marchal) and the extensive feeding that takes place upon the fluids exuding from the resulting puncture.

BEMBICIDAE

The species that comprise this family build their nests in the soil and store them with adult flies, usually of relatively large size, such as the Tabanidae and Syrphidae, though a few species have been reported to prey upon Orthoptera. Wheeler and Dow (1933) cite records of other insect groups that serve as food for the brood of *Bembex*. An African species of the genus was observed to attack lycaenid butterflies, and another in Australia captures adult damsel flies with which to feed its brood. This is presumed to be a temporary expedient made necessary by the absence of the customary food insects. The larvae are fed with freshly killed prey throughout their period of development.

Fabre (1879) has given an interesting account of the habits of *B. tarsata* Panz. of Europe, which may serve to indicate the habits of the family. The female pounces upon her victim with great suddenness, and the rough-and-tumble fight that ensues usually results in the death of the latter through repeated and indiscriminate stinging. The prey is then transported by flight to the nest. Maternal care and feeding continue during the two weeks required for the larva to attain maturity; the number of flies provided for each larva is dependent upon its size.

In this family, the eggs are deposited in the cells and provisions are usually brought in only after the larva has hatched, though some are known to place the egg upon a single victim in the bottom of the cell. The brood tended by each female may comprise a number of larvae.

APOIDEA

HALICTIDAE

The only group in this family that is known to live at the expense of other insects is the genus *Sphecodes*, which appropriates the nests of bees of the genus *Halictus* and of some Andrenidae. Ferton (1923) discusses the relationship existing between *S. monilicornis* Kirby (*subquadratus* Smith) and *H. malachurus* Kirby. The burrow of the latter is always guarded. It is necessary for the *Sphecodes* intruder to kill the defender before taking possession of the nest, and the body of the latter is ejected from the burrow.

NOMADIDAE

The members of this family are largely inquilines in the nests of various solitary bees. Graenicher (1905*b*) presents an account of *Triepoelus helianthi* Rob. as an inquiline in the nests of *Melissodes trinodis* Rob. The egg of *Triepoelus* is apparently deposited in the food material. The first-instar larva is in general appearance like that of *Coelioxys* and its habits are similar. The abdominal segments bear a flat triangular projection at each lateral margin. The very large falcate mandibles are stated to be for use against larvae of their own kind rather than against that of the host bee. Perkins (1919) has reviewed the host preferences of a considerable number of species and finds each of them to be closely associated with a particular host species.

HYLAEIDAE

This is a small family of primitive bees that make their nests in stems of plants, in burrows in the soil, or in various holes and crevices. Several members of the principal genus *Hylaeus* (*Prosopis*) have been observed in Hawaii by Perkins and are stated to live at the expense of others of the family, though the exact relationships have not been determined.

STELIDAE

The bees of this family are inquilines in the cells of other bees, principally the Megachilidae. Attack upon the early stages of the host in the cell is primarily for the purpose of eliminating a rival for the food supply. *Stelis nasuta* Latr. attacks the cells of *Chalicodoma muraria* F. in Europe (Fabre, 1886). These cells are composed of a hard, plaster-like material, 1 cm. in thickness, which the female must penetrate before oviposition is possible. By the use of the mandibles the lid is finally removed, and

several eggs are laid alongside that of the host. When oviposition is complete, the cell is sealed by the invader. The young larvae of host and guest feed side by side without interference; but the *Stelis* larva develops more rapidly, and the host consequently dies of starvation.

In *S. minuta* Nyl. (Verhoeff, 1892), the female deposits the egg upon the food material in the open cell of *Osmia leucomeleana* Kirby before that of the latter is laid. The *Stelis* egg hatches first, and for a time the two larvae feed independently upon the beebread, the parasite at the bottom and the host at the top. Development of the former is more rapid, and eventually it encounters the host larva and consumes it.

The most extended account of the habits of a member of the family is that by Graenicher (1905*b*) on *S. sexmaculata* Ashm., which develops in the cells of *Andronicus productus* Cress. The egg is deposited while the host is in either the egg or the larval stage. The young *Stelis* larva is equipped with long falcate mandibles which extend forward much as do those of a chrysopid larva. It is exceedingly aggressive and, though considerably smaller than the host larva, often being only one-fourth its length, is able to overcome it. The essential food of the intruder is the honey and pollen stored in the cell, and it completes development on this material after killing the host.

MEGACHILIDAE

In this large family belong the leaf-cutting bees and the mason bees, which provision the cells with honey and pollen; but among them are several genera and species that are inquilines in the cells of other members of the family. Graenicher (1905*b*) observed the habits of *Coelioxys rufitarsis* Smith as an enemy of *Megachile* spp. in North America and found that the female bee utilizes the sharp, rigid end of the abdomen in tearing open the inner layer of leaves, from which the cell of the host is constructed, and oviposits through this aperture. The anterior end of the egg remains in the opening, and the opposite end is embedded in the beebread. Oviposition may take place either before the host egg is laid or after the larva has begun its development. The first-instar larva is equipped with enormous mandibles, a very evident adaptation for combat during this stage. Feeding first takes place upon the provisions in the cell, but the larva gradually works its way to the surface, where it encounters the *Megachile* larva and destroys it, irrespective of the stage of development it may have attained.

APIDAE

The family Apidae, which includes the honeybee and various other bees of highly social development, has among its members the genus *Psithyrus*, which live at the expense of the true bumblebees.

DIPTERA

The extensive literature dealing with this order reveals an exceptional diversity not only in habits but in the forms assumed by the immature stages to adapt them to the different conditions under which they develop. The present account is restricted to those representatives of the order which are parasitic or predaceous upon insects and closely related forms, and consequently any consideration of the important groups or species parasitic upon higher animals or involved in disease transmission is excluded.

From the point of view of economic importance, as judged on the basis of attack upon other insects, the order ranks next to the Hymenoptera in the number of species having this habit and in the effectiveness of attack. Among the parasitic families, the Tachinidae is outstanding, and others consistently having the same habit are the Cyrtidae, Nemestrinidae, Pipunculidae, Conopidae, and Pyrgotidae. The Bombyliidae are predominantly parasitic, though many species are predaceous. Parasitic representatives are found in many families that are largely nonentomophagous, such as the Cecidomyiidae, Phoridae, Agromyzidae, Anthomyiidae, and Calliphoridae. The better known predaceous families attacking crop pests are the Tabanidae, Asilidae, Syrphidae, and Ochthiphilidae, but many others have representatives characterized by this habit.

HOST PREFERENCES

The great majority of the parasitic Diptera are primary parasites of plant pests and accordingly are markedly beneficial. Among the Tachinidae, exceptions may be noted in the attack upon adult Carabidae and honeybees, and that upon spiders may perhaps be placed in the same class. The Nemestrinidae, Pipunculidae, and Pyrgotidae are, so far as known, entirely beneficial. The parasitic Bombyliidae are predominantly harmful because of their attack upon the larvae and pupae of beneficial Hymenoptera and Tachinidae, which more than offsets their value as rather infrequent parasites of Lepidoptera and Coleoptera. The Conopidae may be classed as injurious because of their attack upon adult Vespoidea, and the Cyrtidae may likewise be considered harmful because of their parasitization of spiders. Those groups which are predaceous in the larval stage are generally beneficial, as is true also of the adults having that habit. A wide variety of insects are preyed upon by

asilid and other large flies, ranging from scarabaeid beetles to small flies, and it is consequently more difficult to evaluate their effect than that of other families of which the food selection is more restricted. In general, the food sources of the adult predaceous Diptera are determined, first, by size and ease of capture and, second, by their relative abundance in the environment inhabited by the predators.

The host preferences of the parasitic species are varied, lepidopterous larvae being most frequently attacked and then the larvae and adults of the Coleoptera. These two orders are attacked principally by the Tachinidae. Other hosts less commonly attacked are dipterous larvae, hymenopterous larvae and adults, hemipterous, homopterous, and orthopterous adults (occasionally the nymphs also), the nymphs and adults of Dermaptera, the nymphs of Trichoptera, and finally the Arachnida and Isopoda.

The more common families of predaceous habit are the Syrphidae, attacking Aphididae, Coccidae, and other Homoptera, the Asilidae, of which the larvae prey upon various soil-inhabiting insects, and the Bombyliidae, Anthomyiidae, Calliphoridae, and Sarcophagidae, many of which are predaceous in the egg masses of Acrididae. Occasional species of Phoridae, Drosophilidae, and Sarcophagidae develop in the egg sacs of spiders. The predaceous aquatic forms feed upon a variety of insects and other minute animals occurring in their environment. The habits of these forms are given in considerable detail, and with extensive bibliographies, by O. A. Johannsen in his series of memoirs on "Aquatic Diptera," published from 1934 to 1937. A more detailed statement regarding host preferences of all groups is presented under the respective families.

The families that are sufficiently known to warrant a general statement as to the habits of their entomophagous larvae may be listed in the following four groups:

Parasitic only	Predominantly parasitic	Predominantly predaceous	Predaceous only
Cyrtidae			
Nemestrinidae	Bombyliidae	Cecidomyiidae	Rhagionidae
Pipunculidae	Phoridae	Asilidae	Tabanidae
Conopidae	Sarcophagidae	Drosophilidae	Syrphidae
Pyrgotidae	....	Anthomyiidae	Ochthiphilidae
Agromyzidae	....	....	Chloropidae
Tachinidae			

With regard to certain of the above families that contain both parasites and predaceous species there may be a difference of opinion as to

which habit predominates. In the Bombyliidae, for instance, the number of species parasitic upon hymenopterous and other larvae probably exceeds that which is predaceous in egg masses, though the population of the latter may be greater.

Food of Adults.—The food requirements of the adults present a marked variety. Those of the parasitic species feed very generally at blossoms and on various plant exudations, as well as upon honeydew secreted by other insects, and a few species have been noted to imbibe the blood of the hosts in which their eggs are deposited. The adults of groups having predaceous larvae may themselves be predaceous, as in the Therevidae, Rhagionidae, Asilidae, and Dolichopodidae; but those of other groups, of which the larvae are not generally entomophagous, may subsist largely or entirely upon insect food. Among these may be mentioned the Ceratopogonidae, Mydaidae, Empididae, and Scatophagidae.

REPRODUCTION

The manner of reproduction among the parasitic and predaceous Diptera has been the subject of very extensive study and presents as great a range of habit as is found in any other order. The first attempt to systematize this subject was by Townsend (1908), who proposed 5 groups for the Tachinidae, based upon placement of the eggs or larvae with respect to the host. Shortly thereafter, Pantel (1910), following his studies upon the parasitic representatives of the order, but with particular attention to the Tachinidae, increased the number of these groups to 10, using as his basis the reproductive system of the female, the type of egg deposited, the stage of incubation at the time of deposition, and the placement of the egg or larva. His groupings are as follows:

I. Egg macrotype, broadly oval, flattened ventrally, the chorion thick and rigid dorsally and thin ventrally, size proportioned to that of female; deposited upon the body of the host; posterior uterus of gravid female short and broad, occasionally long and narrow (Thrixion). Type: *Meigenia floralis* Meig.

II. Egg microtype, chorion as above, size largely independent of that of female; deposited upon food of the host and ingested by latter; posterior uterus moderately to very long, adapted for partial incubation of a very large number of eggs. Type: *Gonia atra* Meig.

III. Egg large, elongate, not flattened or pedicellate, the chorion thin and flexible; posterior uterus an incubating organ containing a moderate number of eggs; females lacking the chitinized piercing organ; larviporous. Type: *Miltogramma*, *Sarcophaga*

IV. Egg with very thin, uniform chorion; ovarioles numbering 50 to 150, posterior uterus long and coiled, with the eggs lying transversely in several series; first-instar larva with a cuticular armature for protective purposes, indicating a free-living period; larva deposited by female near the host, usually upon its food plant. Type: *Echinomyia fera L.*

V. Egg and larva as in group IV, but the ovaries less numerous, the posterior uterus very long, slender, and coiled (*Bigonicheta, Glaucophana*) or moderately long and distended, the eggs lying transversely in regular series (*Bigonicheta*) or longitudinally and irregularly; larva deposited in vicinity of host.
Type: *Bigonicheta setipennis* Fall.

VI. Egg and larva as in Group IV, with the chorion slightly thicker dorsally; larva without a specialized cuticular armature; ovarioles numbering 15 to 55, posterior uterus of medium length, in one or two corkscrew coils, and more or less distended, with the eggs lying transversely or longitudinally; fully incubated egg deposited upon body of the host. Type: *Cryptophlebia ruricola* Meig.

VII. Female with piercing organ, distinct from the ovipositor, for perforating skin of host; egg not narrowed at posterior pole; posterior uterus slender, elongate, intestiniform, serving as an incubating organ, the eggs lying transversely in a single series. Type: *Compsilura concinnata* Meig.

VIII. As in Group VII, but the ovipositor itself serving as the piercing organ.
Type: *Cercomyia curvicauda* Fall.

IX. Female with piercing organ of variable form and function; egg appreciably narrowed at posterior pole; posterior uterus short and not serving for incubation.
Type: *Hyalomyia, Conops, Oxyptera*

X. Egg with a pedicel at posterior pole, which serves for adhering to the host; ovarioles of moderate number and posterior uterus intermediate between the simple and incubating forms. Type: *Carcelia cheloniae* Rond.

Townsend (1934) has extended this classification through the Muscoidea and enumerates 39 habit groups, the great majority of which comprise some entomophagous species. In addition to the characters and habits utilized by Pantel, he includes also the characters of the first-instar larva. This arrangement, however, is probably of greater value to the taxonomist and to the specialist on insect parasitology than to fieldworkers who may be called upon to study the biology of specific parasites or predators. For general purposes, Pantel's earlier arrangement, which has been widely used, is simpler and more satisfactory. This classification, however, will need to be somewhat revised and extended if it is to include all the parasitic groups of the order, and still further if it is to take in the predaceous forms. Considering those of parasitic habit only, the Pipunculidae, Conopidae, Pyrgotidae, and Agromyzidae (*Cryptochaetum*) apparently all fall in groups VII, VIII, and IX, for the known species consistently insert their eggs into the host body. Most of the Conopidae, however, have stalked eggs. The majority of parasitic Phoridae have the same oviposition habit, though some deposit the eggs externally; yet the females are still capable of puncturing the host with the ovipositor. The parasitic Cecidomyiidae that have stalked eggs do not fall in any one of the groups given, nor do the Cyrtidae, Nemestrinidae, and Bombyliidae. The reproductive systems of a number of these families have not yet been sufficiently studied to permit of definite placement.

There is a very wide range in the reproductive capacity of the parasitic species, this being related directly to the hazards encountered by the eggs and young larvae before the latter gain access to the body cavity of the host. The species that deposit their eggs or larvae in or directly upon the body of the host usually are limited to a few hundred, and several species are known to produce less than 100. Those which deposit them in the general vicinity of the host produce 1,000 or 2,000; in this group are found most of the Bombyliidae and many Tachinidae. Where oviposition is entirely apart from the host or where the eggs must be eaten by the host, the hazards are increased and consequently a higher reproductive capacity is required. Thus the Cyrtidae and the Tachinidae having this habit deposit 2,000 to 6,000 eggs. The extreme is represented by *Echinomyodes*, reported by Townsend to produce approximately 13,000 minute maggots.

LIFE CYCLE

The life cycles of the entomophagous Diptera range from a minimum of about 10 days in *Metagonistylum* and an almost equally short period in various other Tachinidae, Phoridae, Sarcophagidae, and Syrphidae, to the annual cycle required by a great many of both the parasitic and predaceous groups and to a possibly obligatory two-year cycle in some Nemestrinidae. The egg stage is almost invariably short, often owing to partial or complete uterine incubation, and in many species hatching takes place in the uterus or immediately upon deposition of the egg. The shortest larval period is found among the parasitic species, some of which complete feeding in two to four days; this brief period is approached by a few predators also. There is no uniformity in this respect, however, for many species remain inactive within the host body for long periods of time. The pupal stage likewise shows much variation, ranging from one week to nearly a year. The completion of the normal cycle of many species may be interrupted by adverse conditions, resulting in some or all of the individuals going into diapause, which may extend over several years. The duration of adult life is closely correlated with the manner of reproduction, but in the great majority of species it extends to one to two months.

IMMATURE STAGES

A marked degree of specialization has taken place among the immature stages of the parasitic groups of the family as compared with the general predators, and no attempt will be made here to group the latter with respect to egg, larval, and pupal types. For an extended comparative study of the mature larvae and pupae of a considerable number of families, both orthorrhaphous and cyclorrhaphous, the reader is referred to De Meijere (1917).

The Egg.—The egg types are as follows:

1. The *membranous* is the most common; it is distinguished by having a thin and delicate chorion, largely lacking in ornamentation, and ranges in form from elliptical to elongate cylindrical. In the Tachinidae and Sarcophagidae, these eggs usually undergo complete or partial uterine incubation. Relatively few are deposited internally in the host. Other parasitic and specialized predaceous groups having membranous eggs are the Agromyzidae (*Cryptochaetum*), Phoridae, Pyrgotidae, Bombyliidae, Cecidomyiidae, and Nemestrinidae.

2. The *encrusted* egg is similar in form to the above but has a relatively heavy waxy incrustation, which may bear various striate or reticulate markings over the surface of the chorion, giving it a pearly-white color. This type is found generally in the Syrphidae, Drosophilidae, and Ochthiphilidae.

3. The *pedicellate* egg is ellipsoidal to elongate cylindrical in form, with a thin and transparent chorion, and bears a stalk at one end by means of which it is attached to the integument of the host or to an internal organ. In the Tachinidae (genus *Carcelia* only), the stalk is at the anterior end, and the tip is expanded to form an adhesive structure, whereas in the Conopidae it is similarly situated and bears the micropyle at its tip. The egg of the parasitic cecidomyiid, *Endopsylla endogena* Kieff., has a minute stalk that is embedded in the wing of the psyllid host. Partial or complete uterine incubation takes place in eggs of *Carcelia.*

4. The *macrotype* egg is found only in the Tachinidae; it is broadly oval to ellipsoidal in outline, with a thick, tough chorion on the dorsum and sides, and the ventral surface is flat and membranous. This type of egg is attached externally to the integument of the host by its flat ventral surface. Strong adhesion is ensured by a mucilaginous material which accompanies the egg at deposition. Very few of these eggs show any evidence of uterine incubation.

5. The *microtype* egg is, as its name implies of minute size; it may be ovate or almost circular in outline, with the ventral surface thin and membranous, for attachment to a leaf or other surface, and the dorsum and sides heavy, tough, and usually highly sclerotized, with various surface markings. Many genera and species of Tachinidae deposit this type of egg. The eggs of the Cyrtidae, which are of somewhat different form and adhere to the substratum by the posterior end rather than the ventral side, show no embryonic development at the time of deposition, have a long period of incubation, and hatch without the intervention of the host. In the great majority of tachinid species, uterine incubation is complete, but hatching takes place only after ingestion of the eggs by the host. This type corresponds to the microtype egg of the Trigonalidae in the Hymenoptera.

First-instar Larvae.—The first-instar larvae of the parasitic and restricted predaceous groups show a degree of specialization comparable with that of the egg forms. Only the forms that depart from the normal for the higher groups to which they belong will be considered here. The greatest variety in larval forms is found among the Tachinidae, which contains four of the five types listed below.

1. The *muscoidiform* larva is the generalized type of the superfamily and includes the less specialized Tachinidae and Sarcophagidae, the Pyrgotidae, etc. It is a plain maggot, without adaptive characters.

2. The *microtype* larva is that which originates from the microtype egg of many Tachinidae. It is distinguished by its small size, lack of extensive cuticular armature, and the reduction and simplification of the mouth parts. It hatches from the microtype egg in the digestive tract of the host.

3. The *planidium* larva is found generally among the Cyrtidae, Bombyliidae, and Nemestrinidae and frequently in the Tachinidae and in a few species of Sarcophagidae. It is distinguished by a more or less elongate form and a heavy integument,

often highly sclerotized, frequently bearing heavy spines, scales or plates, and long caudal setae, except among the majority of tachinid species. These adaptations provide for an active and relatively long free life before the host is reached. All larvae of this type are followed by a generalized second instar which lacks the above adaptations and is capable of very little ordered movement. (For a discussion of the planidium larva in the different orders, see pages 17–19.)

4. The *vesiculate* type of larva is much less common in the parasitic Diptera than in the Hymenoptera. Among the Tachinidae, it is found only in *Plagia trepida* Meig, and the vesicle is in the form of a large plate occupying the main portion of the ventral face of the last segment. It occurs also in the Pipunculidae and possibly in the Conopidae, though in the latter family the first instar has been little studied and the vesicle has thus far been noted only in the following instars.

5. The *caudate* larva is readily recognized by its paired caudal appendages, which persist in the following instars. Among the entomophagous Diptera, it is found only in the agromyzid genus *Cryptochaetum*, which is parasitic internally in monophlebine Coccidae. This larval form is found in some aquatic or semiaquatic species that are not entomophagous in habit, such as the calliphorid, *Wilhelmina nepenthicola* Vill., of Borneo.

Mature Larvae.—Although there is a marked convergence in form in the mature larvae as compared with the specialized first instar, yet many groups have characters by which they can be readily recognized. We are particularly concerned with the families or lower groups having parasitic larvae and with the highly specialized predators. The general characters by means of which they may be recognized, or at least narrowed to certain limits, are as follows:

Cecidomyiidae.—The head feebly developed and lacking mandibles; body color often red, orange, or yellow; 13 body segments with lateral abdominal spiracles present; of small size.

Cyrtidae.—Body much the widest in the abdominal region, tapering markedly cephalad; a constriction between thorax and abdomen and segmentation evident only anteriorly; anterior and posterior spiracles present, the latter simple in form.

Bombyliidae.—Body crescentic, tapering at both ends, abdomen 9-segmented, with integument glistening and bare; anterior and posterior spiracles present, the latter on the penultimate segment and comprising 8 to 12 openings arranged in a crescent or semicircle around a distinct button; the anterior pair similar but smaller, or fan-shaped.

Phoridae.—Segmentation distinct, though obscured by supplementary folds, the parasitic species usually lacking the fleshy integumentary processes; the bucco-pharyngeal armature in 3 parts with the mandibular sclerite unpaired; anterior and posterior spiracles present, slightly elevated, the latter usually with 4 openings.

Pipunculidae.—Segmentation indistinct and mouth parts reduced; anterior and posterior spiracles present, somewhat elevated, the latter pair situated at the lateral margins of a single heavily pigmented peristigmatic plate, and each usually having 3 openings; some species with the posterior spiracles situated in a pronounced depression.

Conopidae.—Body markedly pear-shaped, with the thoracic segments much attenuated, and the integument clothed with minute setae or tubercles; anterior spiracles often lacking, but when present fan-shaped, with many openings; posterior spiracles very large, convex to hemispherical and heavily sclerotized; the minute spiracular openings arranged in rows or groups, totaling 400 to 700, about a large button; a sclerotized process surmounted by several blunt spines occurs slightly dorsad of each posterior spiracle; paired anal vesicles present in some species.

Pyrgotidae.—Body pear-shaped, with the integument bare and glistening; anterior spiracles stalked and fan-shaped, whereas the posterior ones are very large, of 3

main lobes with many small openings, heavily sclerotized, and usually situated at the dorsal rim of a large median depression.

Agromyzidae (genus *Cryptochaetum*).—Body segments distinct, each with a band of minute setae; the caudal segment with paired tubular tails which may be several times the length of the body; the anterior spiracles dart-shaped or palmate and set in pits; the posterior spiracles in the form of heavily sclerotized, posteriorly directed hooks, with an opening at the base.

Ochthiphilidae.—Abdomen 9-segmented, segmentation indistinct, with integument either bare or having numerous fleshy spines; anterior and posterior spiracles present, the latter consisting of three finger-like structures terminating in simple openings that are borne upon long, cylindrical, diverging processes or stalks.

Sarcophagidae.—Body tapering markedly cephalad, with the posterior end often bluntly rounded; integument clothed with minute spines; anterior spiracles fan-shaped, with 5 to 15 or more openings; posterior spiracles with peritreme incomplete and the slits almost parallel, lacking the button, and situated in the upper portion of a pronounced depression, the rim of which bears fleshy processes of various forms.

Tachinidae.—All general characters variable; integument usually with bands of setae on each segment, which may be complete or broken; anterior spiracles simple, plate-like with several openings, or conical with many minute openings on the distal portion; posterior spiracles usually circular with peritreme complete, the slits most commonly numbering 3 or 4 and radiating from the spiracular button; the number of slits may range up to 30 and are most frequently straight but may be serpentine, branched or broken, or occasionally in the form of numerous small openings, irregularly placed or in rows.

The Pupa or Puparium.—There are two distinct methods of pupation in the Diptera, a fact that serves as the basis for division into two suborders. In the Orthorrhapha, the pupa emerges from the larval skin through a T- or +-shaped fracture, whereas in the Cyclorrhapha the larval skin becomes heavily sclerotized and hardens, forming a puparium enclosing the pupa. The lines of fracture of the puparium occur transversely on the dorsum and venter of the first abdominal segment; and a horizontal fracture, dividing the operculum into an upper and a lower half, extends across the front. The adults of all families of the suborder, except the Phoridae, Platypezidae, Pipunculidae, and Syrphidae, are provided with a ptilinum, by means of which the operculum is forced off. Greene (1925*b*) has presented a tentative arrangement of the muscoid flies based upon the characters of the puparia.

The characters of the pupae or puparia by means of which the principal families may be recognized are as follows:

Cyrtidae.—The body robust, the head markedly ventral, with the thorax greatly arched and longer than the abdomen; prongs, hooks, and spines lacking.

Mydaidae, Asilidae, Nemestrinidae, and Bombyliidae.—The free pupa somewhat elongate in form with the head bearing several pairs of large heavily sclerotized prongs; a row of hooks on each abdominal segment, and the last segment terminating in a pair of prongs. These pupae are capable of considerable movement.

Therevidae.—As in the preceding families except that only two pairs of prongs occur on the head and one prong at the base of each wing pad.

Phoridae.—The dorsum of the puparium much less arched than the venter, with the lateral margins compressed dorsoventrally, giving it distinct boat-like appearance; the surface dull owing to minute setae or to the persistent fleshy spines of the larva; prothoracic cornicles of the pupa extruded and small to large in size; the operculum, which includes the cornicles, may consist of a dorsal and a ventral half or of only the single dorsal plate.

Pipunculidae.—Puparium broadly oblong in outline, occasionally with the caudal spiracular area depressed; the pupal cornicles extruded and minute to very large and conical in form; the operculum in two parts, the dorsal part bearing the cornicles, or they may be situated on the line of fracture.

Conopidae.—Somewhat flattened dorsoventrally, the venter frequently more convex than the dorsum, with the segmentation indistinct and the surface smooth or wrinkled; pupal prothoracic cornicles not extruded; posterior spiracles large and elevated.

Pyrgotidae.—The venter of the anterior region much more convex than the dorsum; posterior spiracles very large and, in most species, situated on the dorsal rim of a pronounced posterior depression; surface bare and shining; pupal prothoracic cornicles not extruded.

Agromyzidae (genus *Cryptochaetum*).—Pointed at the anterior end, with the segmentation distinct and the paired caudal processes of the larva persistent; the anterior dart-like spiracles fully extended and terminal in position, and the caudal spiracles hooked as in the mature larva; pupal prothoracic cornicles not extruded.

Ochthiphilidae.—Oblong in form, flattened ventrally, with segmentation indistinct except in anterior region and the surface dull owing to setae or persistent fleshy spines of larva; stalked posterior spiracles as in the larva; pupal prothoracic cornicles not extruded.

Sarcophagidae.—Oblong to somewhat cylindrical in form, the segmentation indistinct and distinguished from the following family by the large posterior depression within which the spiracles are situated and the margin of which bears fleshy processes or tubercles; spiracular characters as in the mature larva; pupal prothoracic cornicles not extruded.

Tachinidae.—Puparial characters variable, as in the mature larva, usually barrel-shaped; pupal prothoracic cornicles small and extruded in some species.

ORTHORRHAPHA

TIPULIDAE

The crane flies favor particularly a moist habitat; some species are strictly aquatic in habit, and others are semiaquatic. The larvae of the majority of species are plant feeders, though the tribes Hexatomini and Pedecini are predominantly predaceous. Many of those living in an aquatic environment feed extensively upon the larvae of Chironomidae and related insects, whereas some living in the banks of streams and ponds subsist largely upon worms.

CULICIDAE

The larvae of a number of genera and species of mosquitoes are predaceous upon their own kind, in some of which the habit is obligatory. Others attack a variety of insect larvae and smaller animals, including Crustacea, occurring in the pools that they inhabit. The information regarding the predaceous habit in the family has been reviewed by Howard, Dyar, and Knab (1912) and there has been no extended advance in knowledge regarding these species since that time. The larvae of *Psorophora*, *Megarhinus*, *Lutzia*, *Eucorethra*, *Chaoborus*, and *Lesticocampa*

are exceedingly voracious, and even some *Anopheles* exhibit a pronounced cannibalistic tendency. Often the victims are swallowed whole, rather than eaten bit by bit. The species of the genera that have a restricted habitat in holes in trees and similar places are probably entirely predaceous. *Megarhinus* is considered to be the most valuable in controlling infestations of pest mosquitoes, and efforts have been made to introduce various species of the genus into several countries. *M. splendens* Wied. was established in Fiji as a result of importations from Java in 1931.

CHIRONOMIDAE

To this family belong the true midges, of which the larvae of the vast majority of species are of aquatic habit, though some develop in decaying

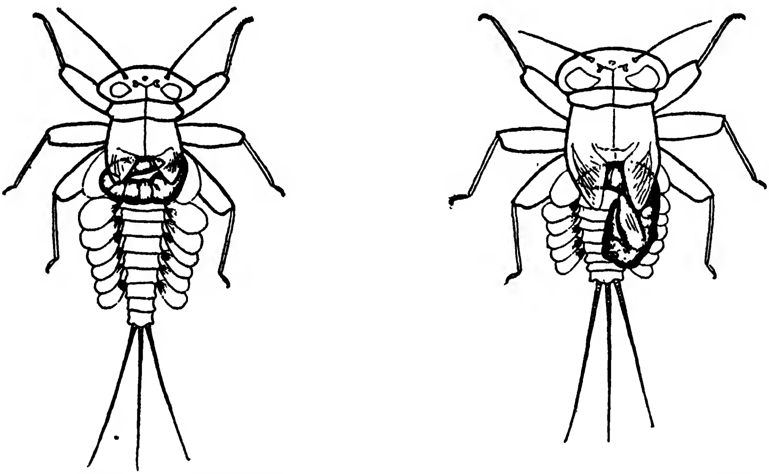


FIG. 157.—Nymphs of *Rithrogena* bearing a larva (at left) and a pupa of *Trissocladius equitans* Claas. (*From Claassen*, 1922.)

vegetable matter or manure or in the soil. The aquatic species feed upon algae, decaying vegetable matter, small Crustacea, etc. Those of the subfamily Tanypodinae subsist mainly upon the larvae of other Chironomidae. *Trissocladius equitans* Claas., however, appears to be a true external parasite of the nymphs of a May fly, *Rithrogena*, and an account of its habits is given by Claassen (1922). Larvae of various instars except the first were found upon the mesothorax under the wing pads, and the head was embedded in the tissues. A sheet of silk is spun over the body and is attached along its entire margin to the body of the host, so that no outside feeding can take place. The larva is thus closely confined to the host body. In its younger stages, the larva lies across the abdomen of the host, but later it assumes a V-shaped position (Fig. 157). Pupation takes place beneath the web, and the pupa

works its way out from beneath this covering and ascends to the surface of the water immediately before the emergence of the adult.

Dactylocladius brevipalpus Galt has recently been recorded as parasitic upon May-fly nymphs of *Rithogena* and other genera in France. The larvae were found only beneath the wing pads, and the species is considered to be a true parasite rather than a commensal (Dorier, 1938).

CERATOPOGONIDAE

The adults of the family, the familiar biting midges, which feed on warm-blooded animals, including man, are parasitic upon other insects in the zoological sense of the term rather than in the restricted meaning employed among entomologists. They feed upon the body fluids of the host insect but do not bring about its death. Several species of *Lasiohelea* and *Forcipomyia* have been taken from the wings of Tipulidae and *Phasmidohelea* spp. from the bodies of Phasmidae, while *Pterobosca* and *Forcipomyia* have been recorded as feeding at the wings of dragonflies. Several species of the latter genus have been recorded as attacking caterpillars. Observations in England and Algeria have shown as many as nine adults of *Atrichopogon meloesugans* Kieff. feeding through the intersegmental membranes of adult beetles of the genus *Meloe* (Blair, 1937). The habits of the larvae of the family are little known, though they are said to feed principally upon the newly hatched larvae of Chironomidae, Culicidae, and Trichoptera.

CECIDOMYIIDAE

The great majority of gall gnats or gall midges, as the minute adults of this family are known, pass through their larval development in cells in plant tissue, and their feeding results in various types of deformity and abnormal growth. A considerable number of species, however, are predaceous in the larval stage upon a variety of hosts, including Aphididae, Coccidae, Aleyrodidae, Thysanoptera, and mites. They are found most commonly as enemies of aphids, scale insects, and mites. Those which attack the Coccidae feed mainly upon the eggs of the soft scales and the mealybugs, though in some species they also attack the nymphs and adults of the latter. A relatively small number of species develop as internal parasites in Aphididae, Tingitidae, and Chermidae. Del Guercio (1919) has listed the genera and species known to prey upon aphids in Italy and gives an extended account of their habits. Barnes (1929, '30, and '33) has reviewed the host preferences of the entomophagous members of the family and presents further information on this subject and on the habits of many species. Because of the limited powers of locomotion of the larvae, these predaceous species are largely restricted to hosts of gregarious habit or, if attacking eggs, to hosts that

deposit them in masses or in numbers sufficient to give an adequate food supply without extensive search. This requirement would appear to reduce their value in controlling crop pests, for they are unable to increase in low host populations and consequently cannot prevent the development of injurious infestations. After a high host population is attained, they may aid appreciably in bringing it under control.

About 50 species of aphid-feeding Cecidomyiidae are listed by Barnes (1929), of which the greatest number belong to the genus *Phaenobremia.* In general, each species limits itself to a single host, and there are very few records of attack upon gall-forming and root-inhabiting aphids.

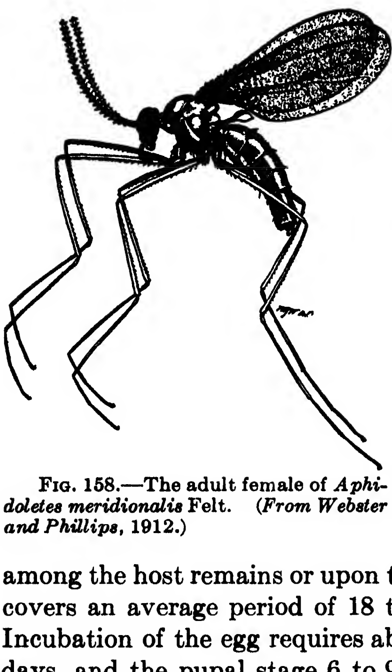


FIG. 158.—The adult female of *Aphidoletes meridionalis* Felt. (*From Webster and Phillips*, 1912.)

Davis (1916) has given an account of *Aphidoletes meridionalis* Felt (Fig. 158), a common predator upon several gregarious species of aphids in North America. The eggs are minute, measuring only 0.1 mm. in length, elongate-oval in outline, and orange in color. The younger larvae puncture the host body from beneath, usually between the legs, whereas the one-third-grown to mature individuals generally feed at one of the articulations of the legs (Fig. 159). The cocoon of loose silk is spun either upon the leaf surface among the host remains or upon the surface of the ground. The life cycle covers an average period of 18 to 20 days, with a minimum of 15 days. Incubation of the egg requires about 3 days, larval development 7 to 11 days, and the pupal stage 6 to 9 days. There are probably at least six generations annually, and the winter is passed in the mature larval stage, and possibly in the pupal stage also, in the cocoon. The adults are largely nocturnal in habit.

Isobremia kiefferi Vouk., a predator of several aphid species, has been studied by Voukassovitch (1932*a*). The eggs are most frequently deposited in groups of four, and most of them are placed at an angle to the leaf surface, rather than horizontally or vertically. Larval feeding appears to be much more deliberate than in *A. meridionalis;* it may require a period of 24 hours for two or three larvae to suck out the contents of a large aphid. The host becomes motionless very quickly after the first feeding puncture is made, and apparently a highly toxic substance is injected into its body by the predator. Larval development is completed in 4 days. In this species, there is an exceptional variation

in the length of the life cycle of the two sexes; that of the females is 16 to 18 days, and that of the males only 8 to 9 days.

More than forty species of Cecidomyiidae are listed by Barnes as being predaceous upon Coccidae, these being distributed among a large number of genera. The hosts most frequently attacked belong to the genus *Pseudococcus,* followed by *Pulvinaria* and other Lecaniinae. In most species, feeding by the larvae is limited largely or entirely to the eggs. An undetermined species, near *Mycodiplosis,* was observed by the author in great abundance upon *Pulvinaria polygonata* Ckll. on citrus in Malaya. Practically every egg mass showed several to a dozen empty pupal skins partly extruded from the waxy covering, and the adults were so numerous as literally to swarm about every infested tree.

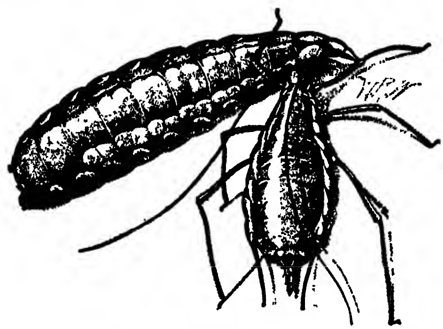


FIG. 159.—A larva of *Aphidoletes meridionalis* Felt attacking an aphid. (*From Davis,* 1915.)

Barnes (1935) records the observations of A. H. Ritchie upon *Schizobremia coffeae* Barnes as an enemy of mealybugs on coffee in Tanganyika. The larvae of this species are found deep in the masses of mealybugs and attached to the ventral surface of the bugs of various instars. They suck out the juices of these individuals rather than of the eggs. The eggs are deposited at random over the mass of bugs or upon the ovisacs.

A number of species are known to attack the diaspine Coccidae, and it is probable that the larvae feed upon the young scales rather than upon the eggs.

Several dozen species are recorded by Barnes (1933) as being predaceous upon free-living mites. Most of these belong to the genera *Feltiella, Mycodiplosis,* and *Arthrocnodax.* They feed upon all stages of the mites, though *A. carolina* Felt, which is rated as the most important of the natural enemies of *Tetranychus* on cotton in the United States (McGregor and McDonough, 1917), confines its feeding to the eggs. A preference is shown for this stage by *A. occidentalis* Felt, also, a common predator of mites infesting citrus in California (Quayle, 1913). The larvae of *A. carolina* consume an average of about 46 eggs per day, whereas *A. occidentalis* may consume up to 380 mites during its larval period of 17 days.

Barnes lists also a considerable number of species, principally of the genus *Arthrocnodax,* that prey upon gall-inhabiting mites and a smaller series that inhabit the galls, possibly in the role of scavengers or inquilines.

Mention has been made by Barnes (1929, '30) of several species that are internal parasites. *Endaphis perfidus* Kieff., which develops in *Drepanosiphum platanoides* Schr., deposits its egg upon the dorsum of the winged aphid, and the newly hatched larva makes its way into the body cavity. Because of its reddish color, the larva can be seen within the body of the living host. When mature, it leaves the host through the anal opening and enters the soil for pupation. *E. agilis* de Meij. is parasitic in the winged adults of *Psylla foersteri* Flor. One to four individuals develop in each host. *Endopsylla endogena* Kieff., which develops internally in the nymphs of *Stephanitis pyri* F., is the most specialized member of the family. It not only feeds internally but differs in habit from the above species by pupating within the body of the host.

Recently Lal (1934) has given an account of *Endopsylla* sp. as a solitary internal parasite of *Psylla mali* Schm., *P. pyricola* Foerst., and others of the genus in Scotland. The egg is oval in form, yellow, and 0.17 by 0.06 mm. in size and bears a minute basal stalk. It is deposited upon the wing of the host, alongside a vein, and the stalk is embedded in the membrane. Hatching takes place in 8 to 13 days, and the young larva crawls to the body and feeds externally for 3 to 4 days. It then burrows through the intersegmental membrane and feeds internally for a further 6 to 10 days; during this time, it completely consumes the body contents. Emergence from the empty host shell is effected through an aperture at the base of the abdomen, and the larva may crawl about over the foliage for 1 or 2 days before it drops to the ground. Here it spins a fibrous cocoon, and the 6-day pupal period is passed therein. There are several generations each year, and the winter is passed in the mature larval stage within the cocoon. The *peregrina* race of *P. mali* is most heavily attacked in the field, the parasitization ranging from 20 per cent in July and early August to 40 per cent in late August and September. The females are more heavily parasitized than the males.

MYCETOPHILIDAE

The fungus gnats are found principally in moist localities, and the larvae of most species probably feed upon fungi. A few species are known to be predaceous in the larval stage. Cook (1913) mentions an undetermined species found in caves in Guatemala, the larva of which forms a slimy web, made up of pendent strands attached to a horizontal cable, suspended from the roof. The prey, consisting mainly of mosquitoes, become entangled in this web and are then eaten.

Mansbridge (1933) has given an account of the larval habits of a number of species of Ceroplatinae and Macrocerinae and reviews the evidence available regarding the food sources of the family. The observa-

tions on the predaceous habit of *Platyura* and related species is confirmed by the shape of the mandibles, the exceptional mobility of the larvae, their solitary habit, and the fact that the web fluid kills other insects. The webs of the species observed are spun upon rock surfaces, under the bark of large rotting logs, beneath boulders or logs on the ground, in fact in almost any location that provides a sufficiently damp environment.

Experiments with active larvae in the webs show that they respond quickly to any movement in the web and will attack anything alive and moving. Periodically, they eject a clear liquid from the mouth upon the prey, and they may also extend the web over it. This web is thickly studded with large droplets of fluid which quickly kills other insects coming in contact with it. The active principle of this fluid has been found to be oxalic acid.

The naked pupa is formed in the larval web. The duration of the larval stage is not known, but the pupal stage of *Platyura* sp. covers 6 to 10 days.

The larvae of *Ceroplatus lineatus* F. apparently have a wide range of food sources; they are reported to feed not only upon insects that become entangled in the web but also on fungus spores and even upon the white-washed surfaces in caves.

The New Zealand glowworm, *Arachnocampa luminosa* Skuse, has attracted considerable attention not only because of the possession of photogenic organs by its larva but because of the means the latter employs to capture its prey. This fly lives in vast numbers in caves, and the larvae feed mainly upon chironomid midges which breed in the water beneath. Edwards (1934) reviews the accounts of several investigators on the habits of this insect. The prey are captured in a manner quite similar to that already described with reference to a Guatemalan species. The larva forms a web of fine threads, to which are added droplets of a glutinous material. There is a strong tube-like central thread, and the larva moves from point to point through this tube. The beaded pendent strands are usually 12 to 30 cm. in length. The light of the larva attracts the midges to the web; and when a victim becomes entangled in a thread this is withdrawn to the central thread occupied by the larva, and the midge is then eaten.

Fulton (1939) has recently presented additional information on the larval habits of several species of fungus gnats of the genera *Platyura* and *Ceroplatus*. One species of *Platyura* forms its webs over the damp earth and rocks in moist locations. The web may be either horizontal or vertical, with several main strands from which the threads extend laterally, and these are 10 to 12 cm. in length. The larva rests upon one of the main strands rather than in a tube and darts out to attack the prey rather than drawing the thread in to the main strand.

STRATIOMYIIDAE

The immature stages of the soldier flies are found under varied conditions, some being aquatic and feeding upon algae, small Crustacea, etc., and others live in decaying vegetable matter. A number of species are scavengers in the nests of insects and lower animals, and a few are found beneath the bark of trees where they feed, in part at least, upon insect larvae.

RHAGIONIDAE (LEPTIDAE)

Many of the snipe flies comprising this family, which includes the two groups that are at times set apart in the families Xylophagidae and Coenomyidae, are predaceous in both the adult and the larval stage. The adults are consistently of that habit, and their prey consists mainly of the adults of other Diptera. A few species are said to have developed the bloodsucking habit. Many are found abundantly only in a decidedly moist habitat, whereas others occur under arid conditions. The larvae are generally of predaceous habit and prey upon a variety of other insects and smaller animals.

The genera *Vermileo* and *Lampromyia* are of particular interest because of the habits of their larvae. The European *V. vermileo* L. is the best known of these owing to the attention given to it by various investigators since the earliest years of entomological research. Two of the most interesting accounts of its habits are by De Reaumur (1753) and Degeer (1776), the latter article having been first published in Swedish in 1752. Full translations of both articles into English, that of the latter being of the original Swedish publication, are given in Wheeler's "Demons of the Dust." The larvae of this and species of similar habit are known as worm lions, to distinguish them from the ant lions of the neuropterous family Myrmeleontidae, with which they have many habits in common.

The pitfalls of the larvae are formed in the dust and sand at the bases of cliffs and in similar situations. They are conical in form, much like the pitfalls of the ant lion, but the *Vermileo* larva lies on its dorsum at the bottom of the pit and encircles any suitable victim that falls within reach and then drags it beneath the sand. As is to be expected, the food of these larvae consists largely of ants.

Wheeler (1930) also discusses the habits of *V. comstocki* Wheeler, which inhabits glacial silt and dust in mountainous sections of western North America. The eggs are deposited in masses of 50 or more which adhere together in rows in the silt or dust, and hatching occurs about eight days later. The young larvae are gregarious, but as growth progresses they become solitary. When in the pit, the larva lies in the inverted

position with the anterior portion of the body across the bottom. The prey consists mainly of the common *Formica fusca* L.

Notes on the habits of several species of *Lampromyia* are given by Wheeler and on *L. sericea* Westw. by Engel (1929). The larva of the African *L. pallida* Macq. differs in habit from others of the genus and from *Vermileo* in holding the body in a vertical position, with the anterior end coiled at the bottom of the pit while waiting for its prey.

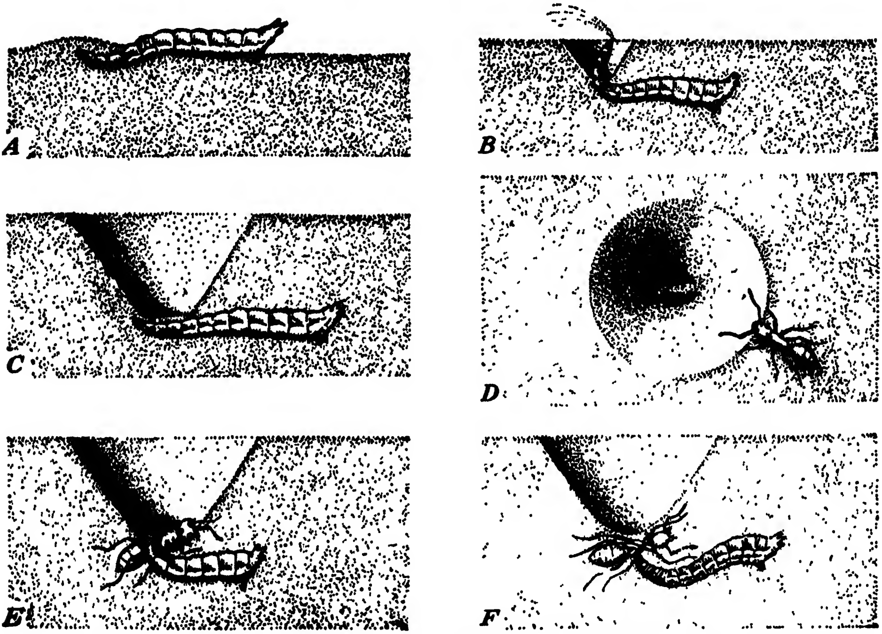


FIG. 160.—Activities of the larva of *Vermileo comstocki* Wheeler. *A*, initial entry into the sand; *B*, tossing out sand in the process of forming the pit; *C*, lying in wait at the bottom of the completed pit; *D*, the pit as seen from above, with the sand-powdered anterior portion of the larva lying across the bottom; *E*, method of seizing the prey; *F*, sucking out the juices of the prey after it has been paralyzed and dragged beneath the sand. (*From Wheeler*, 1930. *By permission of W. W. Norton & Co., New York.*)

The few species of the genus *Chrysopilus* that have been studied differ greatly in larval habits and host preferences from the worm lions that have just been discussed. *C. nubeculus* Macq. is reported to be predaceous in the egg capsules of locusts in Algeria, and *C. ferruginosus* Wied. inhabits decaying roots or plant tissues in the East Indies and the Philippine Islands. The latter is known as a predator on the larvae of the banana weevil, *Cosmopolites sordidus* Germ., and the sugarcane beetle borer, *Rhobdocnemis obscura* Bsd., and has been introduced into several countries in the attempt to control these pests. According to Froggatt (1928), the eggs are deposited in clusters of 16 to 60 in the borer holes in slightly decayed stem tissue. Young larvae have been found

in decaying stems that contained no weevil larvae, and they may subsist in part upon plant food.

Atherix variegata Wlk. is a species of aquatic habit often found in abundance in eastern North America. Britton (1936) describes the finding of large masses of eggs and the remains of many flies on the underside of a bridge in Connecticut. The largest of these masses covered an area of about 50 sq. ft. and was at least ½ in. in depth. The eggs hatch in about six days, and the young larvae drop into the water, where they feed upon various soft-bodied insects and other organisms. The larvae of some species of *Symphoromyia* are also aquatic in habit.

TABANIDAE

The horseflies that comprise this family are known mainly because of the bloodsucking habits of the adults. The larvae are mostly aquatic or semiaquatic in habit and feed upon various types of animal life inhabiting the medium in which they live. A favored food is the larvae of Tipulidae and other groups inhabiting the banks of streams and ponds, and snails and earthworms are also attacked. In Puerto Rico, *Tabanus stigma* F. is reported to develop in drying seaweed, the larvae feeding upon those of sand flies. Several species of *Tabanus* are recorded by Davis (1919) as predators upon the grubs of Scarabaeidae. The eggs of the great majority of species are deposited in large masses upon foliage overhanging water or on stones or other objects near by. In some species, they are found in a single compact layer, the eggs placed vertically and side by side, and in others there are consistently several layers.

CYRTIDAE

The family is represented by a relatively small number of genera and species, and they are very seldom encountered in the field. The adult flies are distinguished by the large humpbacked thorax, the relatively minute head, situated markedly ventrally with respect to the thorax, and often by a pronounced swollen appearance of the abdomen. In several genera, the proboscis is long and is used for sucking the nectar of flowers; but in most forms it is much reduced, and feeding probably does not take place. The flies of some species are exceedingly rapid in flight, though in the great majority they are sluggish and may be recognized by an uncertain and undulating movement. In walking, they are very clumsy, as if the slender legs were inadequate to support the body. The wings are long, and their tips usually drag upon the surface upon which the flies are walking. The adults of many species while resting or ovipositing can be easily captured with the fingers. All species of which the habits are known are internal parasites of spiders, principally of

the families Lycosidae, Salticidae, and Clubionidae, and the earlier records of species occurring as predators in the egg sacs are now believed to be erroneous. Millot (1938) gives a complete list of the known host preferences for the family, these representing seven families, and the majority of the species given are arboreal in habit. The various cyrtid species appear to have a wide host range, each attacking representatives of several families. The more extended studies on the habits of the Cyrtidae are by King (1916) upon *Pterodontia flavipes* Gray, a solitary internal parasite of lycosid and epeirid spiders, and by Millot (1938) upon *Ogcodes pallipes* Latr.

BIOLOGY AND HABITS

Oviposition.—The manner of deposition of the eggs by the flies of this family is of particular interest and has been observed in *O. brunneus*

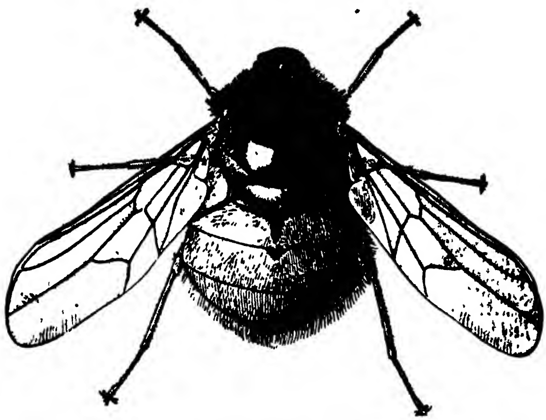


FIG. 161.—The adult female of *Pterodontia flavipes* Gray. (*From Cole,* 1919.)

Hut. (Maskell, 1888), *O. costatus* Loew (Gillette, 1924), *O. pallipes* Latr., *O. varius* Latr. (*fuliginosa* Er.), *Opsebius diligens* O.S. (Cole, 1919), and *P. flavipes*. The first observations were made by F. Stein in 1849, who noted that the eggs of *Ogcodes varius* Latr. were deposited in rows upon *Equisetum*. Maskell writes of seeing females of *O. brunneus* crawling over apple twigs and depositing their eggs in such numbers upon the bark as to give it a black color suggesting a growth of sooty-mold fungus. Konig (1894) states that the eggs of an undetermined species of *Ogcodes* are deposited largely upon dead twigs. *O. pallipes* of Europe deposits its eggs in irregular rows upon the foliage and bark of various trees and also upon *Equisetum*. Gillette reports that a female of *O. costatus* flew into the house and deposited her eggs in irregular rows upon a white cloth. King, in his studies upon *P. flavipes*, was the first to observe oviposition while the female was in flight, and this appears to

be the normal habit of that species. The female hovers on the leeward side of a tree trunk, fence post, or similar object and only a few inches from it and projects her eggs against it with great rapidity. Being partly covered with a mucilaginous material, they adhere to any surface that they may strike. Oviposition while in flight has also been seen under caged conditions in the case of *Opsebius diligens.*

From the foregoing observations, it may be concluded that the majority of species deposit their eggs upon plant surfaces, principally the twigs and branches, while the females are resting or crawling about on the surface. In a number of species, there appears to be a tendency for a number of females to congregate for oviposition; as a result, the plants or branches of trees chosen for this purpose become encrusted with enormous numbers of eggs, making them conspicuous because of the black color. So far as known, oviposition is entirely independent of the presence of spider hosts, though naturally the flies occur in a habitat favorable to a spider population.

The rate of oviposition and total number of eggs deposited by the Cyrtidae are both very high. All species produce several thousand eggs and deposit them in a very short period of time. A female of *P. flavipes* deposited 2,300 within 45 minutes, and a total of 3,977 was secured from another individual. Approximately 3,000 were laid by a single female of *Ogcodes costatus* during a period of four hours. *O. pallipes* deposits a total of 2,000 eggs at the rate of about 1 per minute during her periods of activity. It is quite probable that the egg capacity of some species is at least 10,000.

In this family, as in the Trigonalidae of the Hymenoptera, the eggs are entirely unincubated at the time of deposition, which is in contrast to the fully developed condition of the embryos in the microtype eggs of some of the Tachinidae. The incubation period is relatively long, being 32 to 33 days in *Pterodontia*, 49 days in *Opsebius diligens*, and 30 to 45 days in *Ogcodes pallipes;* the range in the last species being due to different temperature conditions. The fact that these eggs hatch after an incubation period of definite duration also distinguishes them from the microtype eggs of the Trigonalidae and Tachinidae, which must be eaten by the primary or secondary host before hatching can take place. Thus, one factor of loss, the necessity for the egg to be eaten by the host, is replaced by another, involving search for the host by the first-instar larva. The reproductive potentials of the three families mentioned are more or less equal; if this is a reflection of the hazards of survival, it indicates that the losses under the two conditions are likewise approximately equal.

In hatching, the young larvae, or planidia, cut away or force off a well-defined circular cap at the smaller, anterior end of the egg (Fig.

162*A*). This manner of hatching is comparable to that of the dehiscent macrotype eggs of certain Tachinidae.

Habits of the Larvae.—The first-instar larvae, being of the planidium type, are capable of undergoing a free-living period of considerable duration without food. Locomotion is effected either by a looping motion or by jumping. In the latter manner, the larva of *Pterodontia* stands erect upon the caudal disk, which is a specialized structure apparently developed to give a firm hold upon the substratum, and projects itself into space by the sudden downward thrust of the long caudal cerci, bringing them into line with the longitudinal axis of the body from a position at right angles to it. According to Bovey (1936), however, this is accomplished in *O. pallipes* by the lowering of the head to the substratum near the point of attachment of the caudal disk, thus forming almost a circle, following which the body is straightened suddenly. The action is consequently that of a released spring. Cole mentions that the planidia of *Opsebius* are able to crawl in a looping fashion along a single strand of a spider web; this, of course, is a considerable aid in reaching a web-spinning host.

Jumping by the larva, so far as known, is not induced by the presence of the host itself, but it apparently serves to accomplish dispersion. Actual contact with the host is largely by chance, and the planidia, when alert and awaiting the host or stimulated by its presence in the immediate vicinity, assume the erect position.

Little information is available regarding the length of time that the planidia are able to live if contact with a host is not made. Apparently one week is nearly the maximum, which is very short in comparison with that for planidium larvae of other families and orders.

Entry of the planidia into the bodies of the hosts is probably effected through the thin membranes of the articulations of the legs. At this time, they cause appreciable irritation to the host spiders; Cole mentions that *Theridium* adults bearing planidia of *Opsebius* scratched themselves frantically and seemed able to kill a portion of them with the mandibles.

King records the finding of the planidia of *Pterodontia* in all parts of the host body, even in the legs and palpi, though the majority were in the thorax; they persist in this stage, without appreciable growth or direct relation to any host organ, until the following spring. With reference to *Ogcodes pallipes*, it is stated by Millot that the young larvae are usually found in the abdomen during the winter but that they migrate to the respiratory organs in the early spring and the first molt then takes place. A portion of the second stage is also passed in the abdomen, and the second molt occurs there. Brauer (1869*a*) mentions that the larva of *Astomella lindenii* Er., while in the host abdomen, derives its air supply from one of the lung chambers of the host by placing the caudal

spiracles against the lung wall and presumably making a minute perforation. This habit occurs in *O. pallipes*, also, though according to Millot some individuals apparently perforate the abdominal wall instead and thus make direct connection with the outside air. In this latter case, there is evidence of the formation of a respiratory funnel comparable to that of many Tachinidae. Such an adaptation had not previously been recorded in the parasitic representatives of this or other closely related families.

The third-instar larva completes its feeding rapidly and consumes the entire contents of the abdomen of the host. Emergence is effected through a hole cut in the ventral abdominal wall. The host spider usually shows no evidence of parasitism, either by modifications in body form or a change in activities, until a few hours before death. The spider does, however, spin a mat of silk just before death, and Locket (1930) has noted that this is done even by male spiders, an abnormal procedure. He attributes this action in both sexes to increased pressure within the abdomen as a result of the presence of the large parasite body; a measure of relief is probably secured by expulsion of this quantity of silk.

Pupation.—All species of the family pupate outside the host body, in either the web or the burrow or in some sheltered place near the point at which the host died. Emerton (1890) observed that the emerged larvae of *Acrocera fasciata* Wied. suspended themselves in the host web by clinging to a strand with the mandibles; they were supported also by strands beneath the body. A sticky body surface aids the mature larvae in retaining their positions in the web or on a tree trunk. Actual pupation usually takes place the day following emergence from the host. The meconium is cast by the prepupa.

The duration of the pupal stage is short, being 7 days in *Pterodontia*, 6 to 11 days in *O. pallipes*, and about the same in several other species under summer conditions. Emergence of the adult is effected by a median longitudinal break over the prothorax of the pupal shell.

On the basis of the meager information available, there appears to be only a single generation each year, and nine months or more are passed in the first larval stage within the active or hibernating host.

IMMATURE STAGES

The eggs of all species thus far described are of minute size, rarely exceeding 0.25 mm. in length, pear-shaped in outline, and brown to dull black in color. Millot calls attention to an adhesive disk at the larger, posterior end of the egg of *O. pallipes* (Fig. 162*A*) by means of which it becomes firmly attached to any object upon which it may be deposited.

The first-instar larvae have been described for *Ogcodes brunneus*, *O. pallipes* (Bovey, 1936; Millot, 1938), *Ogcodes* sp. (*gibbosus* L. or *zonatus* Er.; Konig, 1894), and *P.*

flavipes. All are distinctly of the planidium type, are 0.3 to 0.4 mm. in length, and have heavily sclerotized segmental plates both dorsally and ventrally. In *Pterodontia*, the body is fusiform, whereas in others it is more elongate, approaching the vermiform. *P. flavipes* (Fig. 162*D*, *E*) is distinguished not only by the exceptionally long caudal setae, or stylets, nearly half the length of the body, which in other species do not exceed the length of the last abdominal segment, but by the palmate scales which occur in transverse rows upon the dorsum of the thorax and ventrally on all body segments except the first and last. In other described species, these scales are replaced

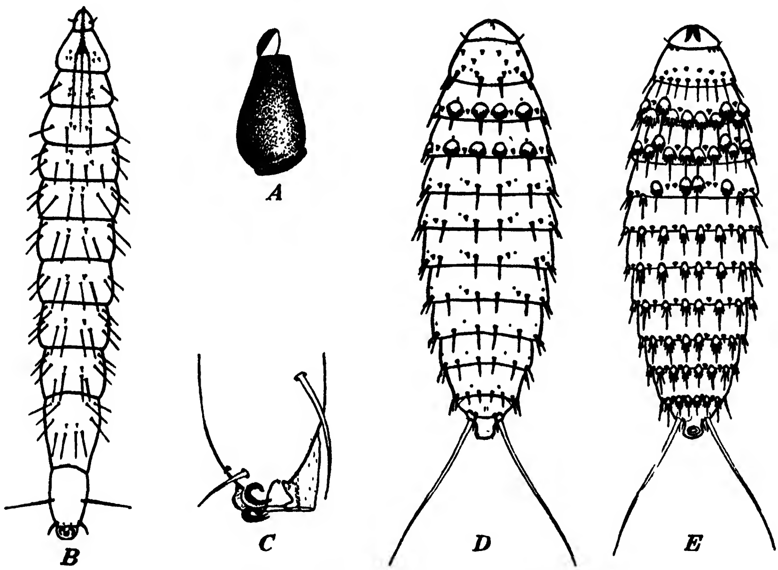


FIG. 162.—Immature stages of the Cyrtidae. *A*, a hatched egg of *Ogcodes pallipes* Latr.; *B*, first-instar larva of same, ventral view (*from Millot*, 1938); *C*, last abdominal segment of same, lateral view, showing the attachment disc and hooks (*from Bovey*, 1936); *D* and *E*, first-instar larva of *Pterodontia flavipes* Gray, dorsal and ventral views (*from King*, 1916).

by simple though heavy spines. *O. pallipes* (Fig. 162*B*) and several others of that genus have two pairs of spines, rather than one, on the caudal segment.

The head is relatively small, and, in *O. pallipes*, the mouth hook terminates in a sharp, upwardly curved point and the three pharyngeal plates are long and slender. The last abdominal segment of *O. pallipes* (Fig. 162*C*) is highly developed as an attachment organ, consisting of the usual adhesive disk and, in addition, three strong hooks, of which the outer two are simple and the median one bifurcate. These structures apparently relate to the manner of jumping and serve to brace and hold the body more firmly than is possible with the disk alone.

There is a difference of opinion regarding the occurrence of an open respiratory system in the first-instar larvae of this family. Konig states that *Ogcodes* sp. bears a single pair of spiracles in two funnel-shaped depressions at the posterior margin of a triangular "shield" on the penultimate abdominal segment. In *O. pallipes*, they are situated dorsolaterally upon the anterior portion of the last segment. King, however, states that spiracles are lacking in *Pterodontia* and that the two crescentic areas at the posterior margin of the eighth abdominal segment, which superficially resemble

spiracular openings, are in reality only the notches in the dorsal plate in which the caudal cerci fit when the larva is in the erect position.

The second-instar larva has not been described for any species, though several authors state that it has a very close resemblance to the third instar.

The fully fed third-instar larvae of *Ogcodes costatus* (Fig. 163) and *P. flavipes* are rather robust, rather indistinctly segmented, and widest in the mid-abdominal region and have a marked constriction between the thorax and abdomen (Kaston, 1937). The posterior portion of the abdomen tapers sharply, and the last segment is broadly conical. The integument is delicate and entirely unornamented except in *O. pallipes*, which has two longitudinal bands of minute "granulations" along each side of the abdomen, and *P. flavipes*, which has pairs of pad-like areas armed with crochets on the ventral surface of the fifth to eleventh body segments. The mouth parts are small and relatively simple.

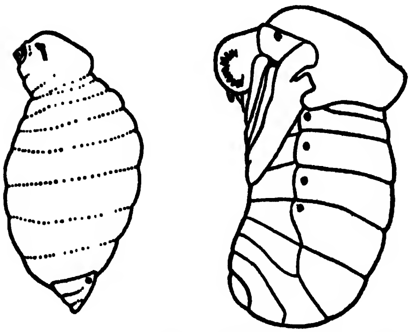


FIG. 163.—The mature larva, after emergence from the host, and the pupa of *Ogcodes costatus* Loew. (*From Kaston*, 1937.)

In *O. costatus* and *O. pallipes*, spiracles are present on the first thoracic and the eighth abdominal segments only, whereas the anterior pair of *Pterodontia* is said to be on the mesothorax. This pair of spiracles is apparently not functional in *O. pallipes* and *Pterodontia*.

There is a marked similarity in form between the pupa of all species that have been studied. The variable characters noted are the crest, or groups of presumed sensory organs on the head, and the number of spiracles. The V-shaped crest of *Pterodontia* consists of a large number of club-shaped processes; in *O. costatus* (Fig. 163) and *O. pallipes*, they occur in two groups on each side of the head. *Astomella lindenii* lacks the crest, or groups of processes on the head, and has a row of spines on the dorsomeson of the thorax. Brauer records six pairs of abdominal spiracles in *Astomella*, several species are said to have four pairs, and King mentions three in *Pterodontia*. Millot found four functional pairs on the anterior abdominal segments of *O. pallipes*, followed by two vestigial pairs on the next segments. He calls attention to the occurrence of only four pairs of abdominal spiracles on the adults of this family and consequently considers it probable that the pupae will be found to have a like number.

NEMESTRINIDAE

Relatively little information is available regarding the host preferences and habits of the members of this rather rare family. Several species have been recorded as parasites of coleopterous larvae, and accounts have been given of two species as internal parasites of locusts. In no instance has the complete life cycle been studied nor have all the immature stages been adequately described.

BIOLOGY AND HABITS

The earliest information relative to the biology, habits, and host preferences of the family is given by Handlirsch (1882, '83) in his account of *Hirmoneura obscura* Meig., a parasite of the pupae of (*Rhizotrogus*)

Amphimallus solstitialis L., which is supplemented by the observations of Brauer (1883, '84). These papers were reviewed and commented upon by Riley (1883*a*, '84).

The adults of *H. obscura* are present in the field during July and early August, and the females were frequently observed depositing their eggs in the abandoned burrows of *Anthaxia quadripunctata* L., and possibly of other coleopterous borers also, in spruce poles, broken branches, etc., from which the bark had been removed or had fallen away. This parasite appears to be closely associated with spruce, and adults could be found in numbers only at the borders of spruce forests where fallen trees or branches were common or in fields bordered by fences of which the poles were spruce. No oviposition was observed in living trees. The female inserts the tip of the abdomen deeply into the exit hole of the beetle and deposits a mass of eggs therein.

Immediately after hatching, the young larvae make their way to the surface of the pole or branch, assume an erect position, and are then presumably blown away by the wind. Riley suggested that they might be carried into the soil by the adult host beetles; but this is improbable, for the normal movements of the latter would not bring them into contact with the young larvae and in any case mere carriage into the soil would be little advantage in establishing contact with a grub or pupa in a suitable stage of development for attack. Brauer noted that the parasitization of *Amphimallus* pupae was highest within 3 m. of the fence of spruce posts and that it decreased rapidly with an increase in distance therefrom.

The second-instar larvae were found in living host pupae during June and those of the third instar a short time later. The host beetle is fully formed and the integument heavily chitinized before death. The parasite is oriented in the same way as the host; and after the fluid contents are completely eaten, it makes a large hole in the venter of the thoracic region and eventually pupates alongside the host remains or partly extruded from the opening. It is assumed that the mature larva persists until the following season, inasmuch as several that had emerged from host pupae during June had not pupated by August.

Under field conditions, the pupae work their way to the surface of the soil just before emergence of the flies. The pupal shells were seen in considerable numbers in the field, each standing upright with the posterior end of the body held in the burrow by the caudal fork and spines.

Brauer speculates on the possible life cycle of *Hirmoneura* as related to that of the host and concludes that it must cover a two-year period, as is the case with the latter. The beetle deposits its eggs in late summer, the larval and pupal stages are completed by autumn of the following year, and the newly formed adults hibernate in their pupal cells and then

appear in the field in June of the second year. The eggs of *Hirmoneura* hatch in July and early August; at this time, no beetle pupae are available, and consequently they must wait until the following May or June to undergo development. If the protracted larval diapause abovementioned is normal, the two-year cycle is obligatory; for larval development is not completed until the season following oviposition, and the second winter is then passed in the mature larval or pupal stage.

How and when the first-instar larvae reach their hosts has not been definitely determined, for the youngest larvae taken from the hosts were in the second instar after the latter had attained the pupal stage,

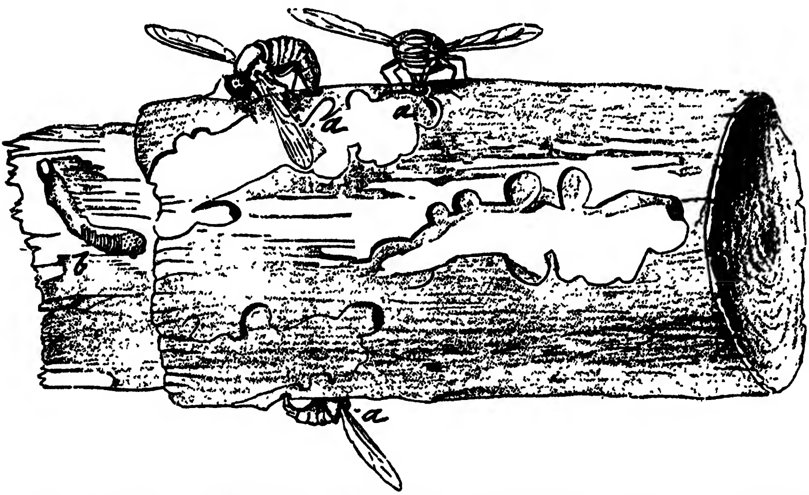


FIG. 164.—Females of *Hirmoneura obscura* Meig. ovipositing in burrows of *Anthaxia* in wood. An egg cluster is shown in the opened burrow at the left. (*From Brauer*, 1883.)

which is about ten months after the hatching of the parasite eggs. Brauer attempts to arrive at a conclusion regarding this point by a comparison with the habits of *Anthrax*, the first-instar larva of which enters the *Agrotis* larva and then awaits its pupation before completing its own development, and *Mantispa*, which hibernates in the first stage and then searches out the spider egg masses the following spring. The first-instar larvae of *Hirmoneura* were found to be exceptionally long-lived; Handlirsch mentions that one remained alive without food from Aug. 17 to Oct. 29. Although this indicates the possibility of living over the winter in the free condition, yet it is more probable that they enter the more mature beetle larvae during the autumn and then remain inactive until after host pupation in the late spring.

Notes are available on the oviposition habit of several other species of the family. Brauer mentions that the South American *H. exotica* Wied. places its eggs in the tunnels of wood-boring bees. More recently,

Spencer (1931, '32) has observed frequently the manner of oviposition of *Parasymmictus clausus* O.S. (recorded as *Rhynchocephalus sackeni* Will.). The females were seen to insert their ovipositors in cracks and holes in telegraph poles, in which no borers of any sort were present, and they remained in that position for one hour or more. Evidence is presented, largely circumstantial, that points to the larvae of cerambycid borers of the genera *Asemum* and *Xylotrechus* as being the probable hosts. Stuardo (1935) observed that the females of *H. articulata* Ph. oviposit

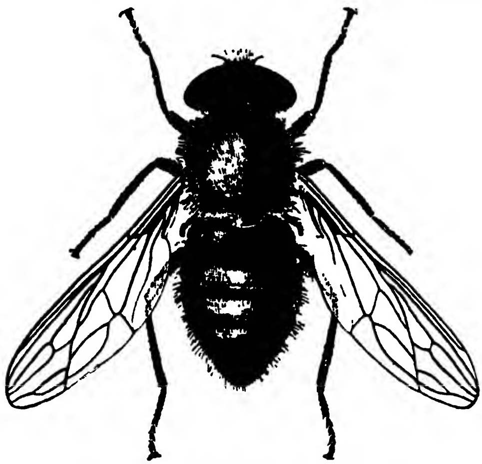


FIG. 165.—The adult female of *Trichopsidea ostracea* Westw. (*From Noble*, 1936.)

mainly during the late morning and early afternoon hours. They are attracted only to posts or poles that lack bark, and the ovipositor is deeply inserted into various holes and crevices. During a period of one hour or more in the one position, a female may deposit a mass of eggs numbering in excess of one hundred.

Incomplete observations have been made on the habits of the later larval stages of two species that are solitary internal parasites of locusts. In South Africa, Potgieter (1929) found the mature larvae of *Symmictus costatus* Loew upon the surface of the ground where a swarm of *Locusta pardalina* Wlk. had settled for the night. An examination of living parasitized locusts indicated that the partly grown parasite larva feeds only upon the body fluids, with little resultant injury to the host, as judged by the normal development of eggs in female locusts. Not only do the eggs develop, but they are deposited normally. At maturity, the *Symmictus* larva leaves the dead host and burrows into the soil to a depth of 2.5 to 5.0 cm. Under favorable conditions, pupation takes place shortly thereafter, and the fly emerges about 14 days later. The mature larva, however, is able to adapt itself to adverse conditions and enters into diapause which, with several individuals held under obser-

vation in dry sand, persisted for more than three and one-half years. Normally, the life cycle is completed in about one year.

The Australian *Trichopsidea ostracea* Westw. is parasitic in adults of the plague grasshopper, *Chortoicetes terminifera* Wlk.; notes on its immature stages and habits have been published by Noble (1936) and Fuller (1938). The larvae are solitary and are found in the abdomen. Unlike *Symmictus*, this parasite leaves the host while it is still alive. The prepupal stage in the soil extends over several months, and the pupal stage lasts for three weeks. The field parasitization was found to be approximately 5 per cent.

IMMATURE STAGES

The eggs of only two species, *H. obscura* and *H. articulata*, have been described. That of the first-named species is 1.5 mm. long, very slender, and slightly curved. The color is at first white, changing during incubation to yellowish-gray. The egg of

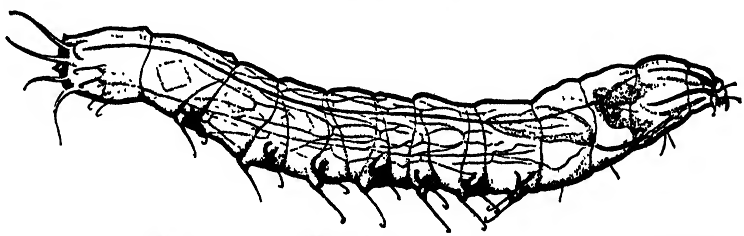


FIG. 166.—The first-instar larva of *Hirmoneura obscura* Meig. (*From Handlirsch*, 1883.)

H. articulata is somewhat larger, measuring 2.0 by 0.25 mm., is curved, and has both ends smoothly rounded. The white color at deposition changes to bluish after a few days.

The first-instar larva of *H. obscura* (Fig. 166), is cylindrical in form and 1.5 mm. in length and has 11 body segments following the head. A distinguishing feature of this larva is the occurrence of a pair of long hooked spines upon the "pseudopods" of the first eight abdominal segments; the ninth segment has two pairs of smaller size. The hooked points of all of these except the two pairs on the last segment are directed caudad. They are said to aid in locomotion in a looping manner. The last segment also bears four pairs of rather fleshy spines which nearly equal the segment in length. The respiratory system comprises a pair of longitudinal tracheal trunks terminating in small simple spiracles situated dorsalaterally on the last abdominal segment. Anterior spiracles are lacking.

The first-instar larva of *H. articulata* is described and figured by Stuardo, and is identical in all principal characters with that described above.

The second-instar larva of *H. obscura*, as described and figured by Brauer, is elongate-cylindrical, with the posterior end of the body broadly rounded. The integumentary armature of the first instar is lacking. The tracheal system is unchanged, though the posterior spiracles now have a large central button with a large number of short linear slits radiating outward in a complete circle.

What is presumably the second instar of *T. ostracea* was observed by Fuller and is apparently quite similar to that of *H. obscura*. Anterior spiracles are lacking, and the posterior spiracles (Fig. 167*A*) are circular in form with 9 to 10 elongate-oval slits radiating from the central button.

Potgieter's brief description of the supposed second-instar larva of *Symmictus costatus* reveals a form entirely different from that of *Hirmoneura*. This larva possesses a tail approximately twice the length of the body, and is comparable to that of the rat-tailed Syrphidae; this organ is said to serve as a means of attachment to the integument of the host and presumably functions in respiration. This adaptation is so markedly at variance with the known larval forms of this and all closely related families that a more thorough study would be highly desirable. If a respiratory connection is made by means of an opening in the integument, it would be expected that an integumentary funnel, or respiratory sheath, would be formed. So far as is known at present, this is found only in the Tachinidae and a few Sarcophagidae, with some indication of its occasional appearance in the Cyrtidae.

The mature third-instar larva of *H. obscura*, as described by Handlirsch, is 22 mm. in length and measures 5 mm. at its widest point. The segmentation is distinct, and the abdominal segments bear various ridges, welts, and folds. The caudal segment is more heavily sclerotized than those preceding it and bears fleshy transverse dorsal and ventral lobes or ridges. The posterior spiracles are situated on the inner side of the upper lobe. The respiratory system has only this one pair of spiracles, which is in marked contrast to the number found in related families. The paired mouth hooks are short but stout, and the three pharyngeal plates are long and slender.

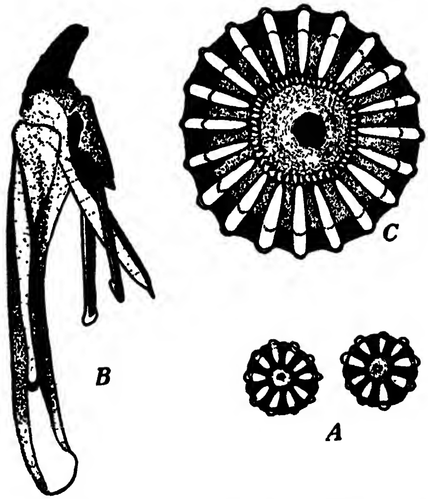


FIG. 167.—Larval details of *Trichopsidea ostracea* Westw. *A*, posterior spiracles of the young larva; *B*, mouthhooks of the mature larva; *C*, spiracle of same. (*From Fuller*, 1938.)

The third instar of *T. ostracea* is pale-yellow in color, 9 to 17 mm. long, and much the widest in the posterior abdominal region. Each body segment bears one or two rows of fleshy processes dorsally and ventrally. The posterior spiracles (Fig. 167*C*) are circular, with 20 linear slits radiating outward from the central button. Functional anterior spiracles are lacking, but vestigial ones are present on the first thoracic to the seventh abdominal segments.

The pupae are similar to those of related families in the head armature and the hooks and spines borne on the abdomen. In *H. obscura*, there are two long, slender, curved prongs at the anterior ventral margin of the head, and above them is a pair of conical processes. The first three abdominal segments bear a ring of forwardly directed hairs, which occur ventrally on the following segments, also; these latter segments bear dorsally a transverse row of heavy curved spines, or hooks, which are likewise directed cephalad. Distinctly raised spiracles occur on the prothorax and the first seven abdominal segments. The last abdominal segment terminates in a pair of large, laterally directed prongs, of anchor-like form.

MYDAIDAE

The adult flies of this family are among the largest of the Diptera and are predaceous in habit. The larvae of some species live in decaying

wood, and some of them feed upon coleopterous larvae which are found in that medium. *Mydas clavatus* Drury is reported to have this habit (Greene, 1917). The pupae of the family are similar in form to those of the Asilidae and Bombyliidae.

ASILIDAE

The so-called robber flies of the family Asilidae are predaceous in both the larval and adult stages. The larvae, which live in the soil or in decaying wood, feed mainly upon the various stages of any soft-bodied insects that they encounter, including locust eggs. In certain localities, they are sufficiently abundant to destroy an appreciable

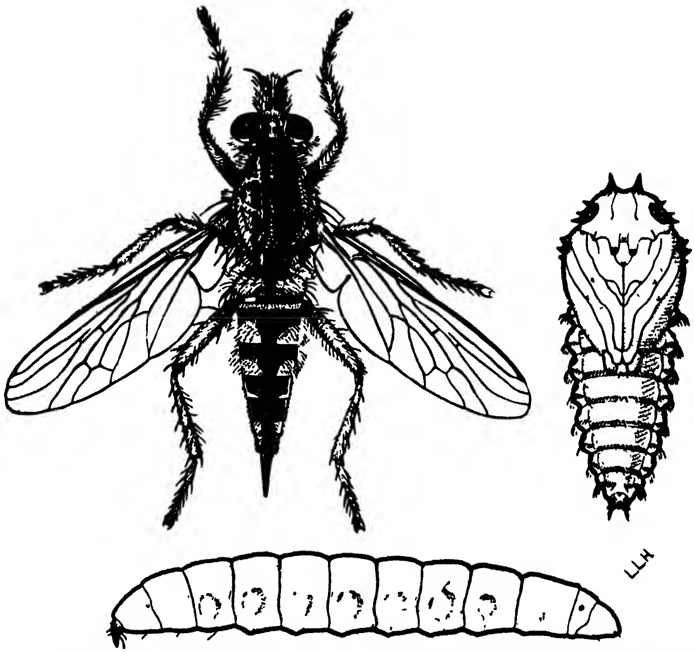


FIG. 168.—The mature larva, pupa and adult of *Erax lateralis* Macq. (*From Titus*, 1905.)

portion of the white-grub population. A few species are said to feed upon the roots of plants. *Hyperechia nigripennis* Wied. and others of the genus are believed to be parasitic externally upon the larvae and pupae of *Xylocopa* (Poulton, 1924; Engel, 1929).

The adult flies are often very large, and in the majority of species the body is rather elongate and the abdomen slender and tapering. Many species are clothed with a dense pubescence.

It is uncertain whether the family should be considered as predominantly beneficial or injurious. The larval feeding habit is largely beneficial, for the bulk of other insects encountered in the soil are plant

feeders. Davis (1919) records several species as predators upon scarabaeid grubs. The adults are exceedingly voracious and feed more or less indiscriminately, destroying many parasitic and predaceous flies and wasps as well as beetles, etc. Their efficiency in hunting is illustrated by the frequent capture of *Vespa* and *Polistes* adults, which are themselves aggressive fighters. *Proctacanthus longulus* Wied. and *Erax interruptus* Macq. are stated to feed principally upon grasshoppers. According to Greene (1917), the larvae of *Dasyllis thoracica* F. occur in decaying wood, where they prey upon other larvae inhabiting that medium, and are themselves secondary wood borers. Hobby (1931, '33) has given an extended list of the insects preyed upon by the Asilidae in England.

Several species of the family are serious enemies of honeybees in Europe and America. Bromley (1934) states that *Saropogon dispar* Coq. is the most injurious of a number of species frequently found in the vicinity of apiaries in Texas and that more than 700 of these flies were destroyed in one bee yard in a period of three days. Considerable loss results from their attack, particularly upon the virgin queens. *P. milbertii* Macq. (*Asilus missouriensis* Riley) likewise preys upon honeybees in Missouri, where it is known as the "bee killer" (Riley, 1870). The reduction in population of various wild bees as a result of attack by various species of the family may result injuriously owing to less complete pollination of blossoms.

The eggs of *Promachus yesonicus* Bigot of Japan are deposited in masses of considerable size upon grass blades and are covered with a considerable quantity of soft chalky-white material. Many other species have the same oviposition habit. *Mallophora orcina* Wied. is said to deposit its eggs in a small cluster in a shallow hole in the soil, which is covered by the female after oviposition is completed. Davis describes a similar oviposition habit in *P. vertebratus* Say. In the few species that have been studied, the incubation period is relatively short. *Laphria flava* F. is reported to deposit its eggs in crevices in pine trees, in which the larvae live under loose bark.

The larvae are vermiform in all instars, and the pupa is of the free type similar in general characters to that figured for the Bombyliidae. These pupae also have the habit of coming to the surface of the soil just prior to emergence of the adult.

The life cycles of the more common species range from one to three years, with the adults present in the field throughout the summer. *Erax interruptus* is stated to have a pupal period of 20 to 26 days.

THEREVIDAE

Very little is known regarding the habits of the members of this small family. The adults are said to be predaceous principally upon

other Diptera, and the larvae live in sandy soil and are predaceous upon earthworms and various soft-bodied insects. The larvae of *Phycus brunneus* Wied. occurring in bat dung in India are said to feed upon dermestid larvae (Isaac, 1925). Goetze (1932) considers that the supposed predaceous habit of the larvae is still open to question. He mentions a rye field that showed extensive root injury, in which only therevid larvae were present in numbers. In laboratory tests, however, they did not feed upon the roots.

The immature stages are similar to those of the Asilidae. The first-instar larvae are vermiform, with 20 apparent segments, due to "intersegments" between the first six true segments of the abdomen. Prothoracic and caudal spiracles are present. The mature larva of *Psilocephala sequa* Wlk. (Bhatia, 1934) is likewise elongate and bears the spiracles at the posterior margin of the first thoracic segment and at the anterior margin of the fourth "segment" from the end of the abdomen. The pupa has heavily sclerotized processes upon the antennal sheaths and at the base of each wing sheath. The abdominal segments each bear a ring of long spines at the posterior margin, and the last segment is produced into a pair of large, heavily sclerotized processes.

SCENOPINIDAE

This is a small family, the adults of which are known as window flies. The immature stages live in decaying fungi and wood and are also found at times in furniture and beneath carpets. *Scenopinus fenestralis* L., the most frequently encountered species, has the latter habit and is said to be predaceous upon carpet-beetle larvae. The larvae of some species inhabit fungi and decaying wood and feed upon other insects found in these media.

BOMBYLIIDAE

The family Bombyliidae comprises the well-known bee flies, which are usually stout-bodied and densely clothed with a fine pubescence and usually have partly clouded wings. The adults of the genus *Systropus* are distinguished from others of the family by their slender form, which gives them a marked resemblance to the Conopidae. The family contains a large number of genera and species and is found commonly in all parts of the world.

HOST PREFERENCES

The host preferences of the members of the family are exceedingly varied, though the species themselves are confined within relatively narrow limits. Information regarding the general host preferences of the family has been presented by Bezzi (1924) and Painter (1932). A

considerable number are predaceous in the egg capsules of locusts, and it is in this capacity that the family is best known. This habit was first discovered by Riley (1880) in his studies on the Rocky Mountain locust. Many species are external parasites of the larvae, prepupae, and pupae of Hymenoptera (Vespoidea, Sphecoidea, and Apoidea and more rarely of Ichneumonoidea and Tenthredinoidea) in their cells or cocoons, and a few species are parasitic externally upon soil-inhabiting coleopterous larvae or pupae (Cicindelidae, Scarabaeidae, and Meloidae). Some of the species that attack locust egg pods also develop upon the pseudonymphs of meloid species that are predaceous upon the same host stage. Other species are also recorded as having a wide host range. *Villa alternata* Say has been reared from both noctuid and tenebrionid pupae. Zackvatkine (1934) records *Anastoechus mylabricida* Zack. as attacking prepupae and pupae of *Zonabris* and occasionally the larvae of Carabidae and other soil-inhabiting insects. *Anthrax oophagus* Par. attacks not only locust eggs and *Zonabris* larvae and pupae but occasionally develops as a secondary parasite through other Bombyliidae. *Systropus conopoides* Kunckel and others of that genus are solitary parasites of the larvae of the Eucleidae in their egg-like cocoons. A number of species develop internally in larvae or pupae of other Lepidoptera (Noctuidae, Pyralidae, Tineidae and Tortricidae), in larvae and pupae of Coleoptera (Tenebrionidae), and in pupae of Diptera (Asilidae, Tachinidae, and Muscidae).

In respect to the species that develop internally, it has not been determined what stage of the host is initially attacked by the first-instar larva. In some cases, at least, the species that parasitize lepidopterous pupae enter the active caterpillar while it is still feeding. Allen (1921) reared *Anthrax lucifer* F. from pupae of *Laphygma frugiperda* S. & A. that had developed from larvae collected and isolated when about half-grown. The first-instar larvae had consequently entered the caterpillars prior to that time, though extensive feeding and development did not take place until after pupation. In discussing the species that attack Tachinidae, Baer (1920) expresses the belief that the young larvae enter the mature maggots at the time when they have left their hosts and are entering the soil for pupation. There is more reason to believe, however, that they penetrate the puparial wall directly. It has not yet been established that these species are true internal parasites, for they may feed externally upon the pupa within the puparium.

Hemipenthes is stated to be a hyperparasite of Lepidoptera through various Ichneumonidae, from the cocoons of which several species of the genus have been reared. Here, again, there is considerable doubt as to the true host relationships. The first-instar larva may enter the body of the caterpillar and thus gain access to the ichneumonid larva, or it may attack the latter directly and only after the cocoon has been formed.

As a whole, the family can probably be regarded as more beneficial than injurious owing to the extensive attacks of many species upon the egg masses of Acrididae. Aside from the few species which attack Lepidoptera, Tenebrionidae, Scarabaeidae, and Tenthredinidae and those which attack *Glossina*, the long list of hosts of the parasitic species consists of insects that are themselves entomophagous in habit.

BIOLOGY AND HABITS

The adult flies are most commonly observed during periods of bright sunshine, though some species show a preference for a shady habitat.

Fig. 169.—The adult female of *Hyperalonia oenomaus* Rond. (*From Clausen*, 1928.)

With few exceptions, they are flower feeders and subsist upon nectar and pollen, though several genera are stated to lack functional mouth parts and presumably do not feed.

Oviposition.—There is a considerable variation in the manner of oviposition among the species of the family. Of those which develop in acridid egg pods, Zackvatkine (1931) mentions that *Callistoma desertorum* deposits its eggs in holes and fissures in the soil and that 80 to 100 may be laid simultaneously. The females of this species are capable of producing 1,600 to 2,000 eggs. Those of *Cytherea setosa* Par. are deposited in groups of 1 to 5 on the surface of the soil in shaded places, or in crevices. *A. oophagus* Par. and *A. jazykovi* Par. oviposit in the same way. De Lepiney and Mimeur (1930) concluded that the female of *Glossista infuscata* Meig. probably inserts her eggs directly into the freshly formed egg pod, though this was not definitely established. In reference to *Bombylius variabilis* Lw., it is recorded by Melis (1934) that the female apparently oviposits while in flight, merely touching the

abdomen to the ground near an ovipositing locust or a newly formed egg pod.

The species that attack hosts contained in open burrows or cells apparently adopt a method of oviposition quite different from that of the species that develop as egg predators. Dufour (1858) states that the female of *B. major* L. inserts the egg into the entrance of the nest of *Andrena* during the absence of the female bee. According to Seguy and Bandot (1922), the female of *B. fugax* Wied. projects the egg into the nest opening of *Panurgus* while she is in flight, and the same habit is recorded for *Hyperalonia morio* F., which parasitizes *Monedula*. Painter (1932) records experiments in inducing oviposition by *Villa* sp., which develops in the cells of solitary bees. The eggs were readily projected into glass vials buried in the soil to simulate the nest openings of the host.

Habits of the Larvae.—Immediately after hatching, the young larva is under the necessity of searching out its host. In most cases, this search is not extensive, inasmuch as the egg is deposited in the immediate vicinity of the host individual to be attacked. The larva is well-equipped for movement in the soil and thus has little difficulty in reaching host stages that are found there. The species that develop as predators in locust-egg capsules are usually solitary, though a few are gregarious. In the case of *B. variabilis* Lw., it is stated that after consuming one egg mass the larva searches about in the soil for a second one. Species such as *A. trifasciata* Meig. (Fabre, 1886) which develop upon the larvae of the mason wasps are under the necessity of penetrating an exceedingly hard cell wall before the host can be reached, and those which attack the parasitic Hymenoptera may possibly have to make their way into the cocoon. Feeding then begins, and larval maturity is quickly attained in the case of those species which attack inactive host stages. In *A. anale*, the larva first attaches itself to the venter of the thorax of the third-instar *Cicindela* larva (Shelford, 1913). A thickened chitinous ring is formed around the feeding puncture. Growth is slight until the host forms its pupation cell, which may be eight months after the parasite larva has attached itself. From this point onward, development is rapid. The larvae of *Exoprosopa fasciata* Macq. (Richter and Fluke, 1935), which parasitize *Phyllophaga* pupae, attach themselves to the venter of the pupa. *Sparnopolius fulvus* Wied. has been reported occasionally as a parasite of grubs of the same genus.

The young larvae of *Spogostylum delila* Lw. (Niniger, 1916), which develop in the cells of *Xylocopa*, are often found in the cells even before the host eggs have hatched. They may wander about over the food mass for one month or more, feeding promiscuously, before settling down, during which period very little growth takes place. A definite feeding position is finally taken upon the third or fourth abdominal segment of

the bee larva, and the body contents are then consumed in about five days. The first-instar larva of *B. pumilis* also has the habit of feeding upon the food material stored in the cell of its host, *Colletes daviesana* Smith.

Pupation and Emergence.—The place in which pupation occurs differs markedly among species and is of course dependent upon the kind and stage of host attacked. The larvae that develop in acridid egg capsules quite consistently leave the capsule and form a pupal cell in the soil at some distance from it. The larva of *Systoechus albidus* Lw. (Potgeiter, 1929) burrows downward 8 to 20 cm. in compact soil and forms a distinct cell. *E. fasciata* on *Phyllophaga* pupae and *A. anale* on *Cicindela* larvae pupate in the host pupation cell. The species that are external parasites of the larvae of solitary bees, wasps, and sawflies pupate within the host cell or cocoon, and those upon or in Diptera do so within the puparium. The internal parasites of lepidopterous and coleopterous pupae transform within the pupal shell of the host.

Just prior to the emergence of the adult fly, there is a period of pronounced activity of the pupa, the purpose of which is to free it from any covering or enclosing wall and to permit the adult fly to emerge directly into the open air. The species found in the soil come to the surface, after traversing 1 m. or more of soil, and at least the anterior portion of the body protrudes from the burrow before the adult fly emerges. Pupae contained in cells or cocoons must cut away an opening equal to the body width, and this involves repeated rotations of the body to rasp away a hole sufficiently large to permit complete or partial extrusion. Those which pupate within the pupal remains of the host rupture the body wall ventrally in the thoracic region and escape. Those contained in puparia either force off the operculum or cut away a portion of the puparial wall. In each case, the repeated bending and twisting of the abdomen cause the head crown of the pupa to penetrate the soil or rasp away the cocoon or cell wall confronting it.

Kunckel d'Herculais (1905), in discussing the emergence of *Systropus conopoides* from eucleid cocoons, mentions the ability of the pupa to fill its digestive tube with air, thus greatly inflating the body and aiding in emergence. This inflation is not associated with a dilation of any part of the tracheal system. It gives the body greater leverage within the confined space of the cocoon, and pressure is essential to the efficient use of the specialized cutting structure on the head.

The adult fly emerges from the pupal skin through a longitudinal split along the dorsum, and this is accomplished with extreme rapidity. It is stated by Austen and Hegh that the time elapsing between the cessation of movement of the pupa of *Thyridanthrax lloydi* Austen and the flight of the fly is only two or three minutes.

Life Cycle.—The life cycles of the Bombyliidae quite consistently cover a full year in those species which occur in temperate regions, whereas it may be completed in two months or less by the tropical species. Adverse conditions, particularly a lack of moisture, have a pronounced influence upon the development of many species and cause them to go into diapause for long periods. Potgieter mentions the keeping of mature larvae of *Systoechus albidus* in dry sand for four years; after this, completion of development and emergence were quickly secured when sufficient moisture was provided. This adaptation is advantageous to the species under arid conditions.

The duration of the incubation period has been definitely determined only in the case of *Bombylius fugax,* in which it is stated to cover 8 to 12 days. In *Anastoechus mylabricida* Zack. (Zackvatkine, 1934), however, the egg is said to persist through the winter. The larval feeding period represents only a comparatively small portion of the entire cycle. In *Hyperalonia* sp. studied by Dutt (1912), the consumption of the mature *Pseudagenia* larva is completed in 3 to 4 days, followed by a resting period of 5 to 6 days, whereas *H. oenomaus* requires 5 to 8 days for its feeding. In most other species, however, a considerably longer period of feeding prevails, about one month in *S. albidus* and approximately seven weeks in *Spogostylum delila* Lw. Copello (1933) states that the first-instar larva of *Hyperalonia morio* reaches its *Monedula* host in the late autumn, feeds sparingly until spring, and then rapidly consumes the prepupa the following spring. *B. variabilis*, *B. pumilis*, and *Hyperalonia* sp. are reported to pass the winter as first-instar larvae, though the great majority of species hibernate as mature larvae. An exceptional habit occurs in *Anthrax anale,* in which the second-instar larva is found during the winter period (Shelford, 1913).

The duration of the pupal stage ranges from a minimum of 7 to 9 days in *Systoechus albidus* to slightly less than one month for *H. oenomaus,* with 12 to 16 days as the normal for the majority of species. Occasional individuals of a few species hibernate in this stage.

Field Parasitization.—The field parasitization recorded for a number of species of Bombyliidae indicates a considerable degree of effectiveness, though almost invariably there is a marked variation in this respect over the range covered by the hosts. In the species attacking soil-inhabiting hosts, soil conditions appear to be the principal factor governing effectiveness. A high mortality may be brought about in one locality, whereas another near by may show almost complete absence of attack. Usually, the range of the parasitic or predaceous species is more limited than that of the host.

Among the species that attack the egg pods of Acrididae, *Glossista infuscata* Meig. is reported by de Lepiney and Mimeur to destroy up to 85

per cent of the eggs of *Dociostaurus maroccanus* Thbg. in Morocco, while Zackvatkine, as a result of his observations on several species in Turkestan, estimates that approximately 20 per cent are destroyed each year by *Callistoma desertorum* and up to 40 per cent by *Cytherea setosa* Par. Potgieter mentions the finding of 1,143 larvae of *Systoechus albidus* in 1 sq. yd., which contained more than 100 egg pods of *Locustana*. A considerable number of larvae develop in each mass of eggs. In his observations on *Aphoebantus hirsutus* Coq., Wilson (1936) found 62.4 per cent of the egg pods of *Camnula pellucida* Scudd. destroyed by the predator. This species and most others attacking similar hosts are solitary in habit. All the eggs in the cluster may not be consumed, but those remaining do not hatch, owing to desiccation and the entry of disease organisms. In areas that showed heavy attack by *Aphoebantus*, the hopper emergence the following spring was negligible. This predator is quite scarce in arid sections having a sparse vegetation.

When other groups of hosts are attacked, the parasite population may also be quite high, as shown by the parasitization of 55 to 65 per cent of the cocoons of *Tiphia* sp. by *H. oenomaus* in India (Clausen, 1928*b*) and 18 to 25 per cent of the pupae of *Laphygma frugiperda* by *Anthrax lucifer* in the southern United States. Copello states that the parasitization of the larvae of *Monedula surinamensis* is very high among those which mature during December to February.

IMMATURE STAGES

The eggs of the Bombyliidae, in so far as they are known, present no adaptive modifications whatever. They are oblong in form, are at times slightly curved, have both ends smoothly rounded, and are two to four times longer than broad. They are relatively large, measuring 1.0 by 0.25 mm. in *Hyperalonia morio* F. and *Bombylius fugax* Wied. Apparently all species cover the egg with a coating of mucilaginous material to which soil particles adhere at the time of deposition.

The first-instar larva of *H. oenomaus* (Fig. 170*A*) (Clausen, 1928*b*) is vermiform, 0.9 mm. in length, and grayish-white in color. There are 12 body segments which, with the exception of the last, are of equal width. The head capsule is heavily sclerotized, its anterior margin is serrate, and it bears a number of heavy setae. Each thoracic segment bears a long slender spine, directly laterally, at each lateroventral margin. The caudal segment bears a pair of slender spines, which are about one-third the body length, dorsolaterally, each arising from a distinct conical protuberance. Intersegmental welts occur lateroventrally between the abdominal segments. The two pairs of spiracles are of simple form and are situated at the anterior margins of the first thoracic and the last abdominal segments, respectively.

The described first-instar larvae of other species of the family are similar in all essential respects to the larva of *H. oenomaus*. That of *B. pumilis* Meig. described by Nielson (1903) is stated to have the lateroventral welts at the anterior margins of the second to sixth abdominal segments only. The posterior spiracles of this species are elevated and occur at the posterior margin of the eighth abdominal segment, rather than on the last segment. No thoracic spiracles were detected. The larva

of *B. fugax* Wied. (Seguy and Baudot, 1922) is similar to *B. pumilis* in all characters mentioned. The mouth hooks of this species are stated to be paired and articulated.

The second-instar larva has been described for *H. oenomaus* and *B. pumilis*. The body is rather maggot-like as contrasted with the vermiform first-instar larva. That of *H. oenomaus* (Fig. 170*B*) has 12 distinct body segments with the intersegmental constrictions very pronounced, is widest in the mid-abdominal region, and bears no spines or setae. The color is mottled white and yellow, the latter due to the large and numerous fat bodies which are visible through the transparent integument. The two pairs of simple spiracles are situated at the posterior margin of the first thoracic and eighth abdominal segments, respectively. The larva of *B. pumilis* is similar except that the body segments are of nearly uniform width and the segmentation is not pronounced.

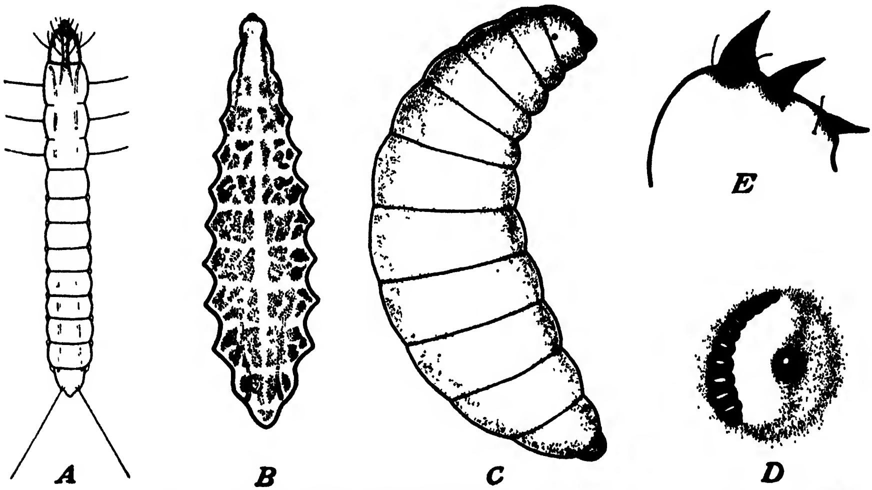


FIG. 170.—The immature stages of *Hyperalonia oenomaus* Rond. *A*, *B*, and *C*, first-, second-, and third-instar larvae; *D*, posterior spiracle of mature larva; *E*, head crown of the pupa. (*From Clausen*, 1928.)

The third-instar larva has been described for only a few species. That of *H. oenomaus* (Fig. 170*C*) has 12 body segments and is somewhat elongate, curved, and widest in the mid-abdominal region. The integument is smooth and glistening, without setae or other ornamentation. The posterior spiracles (Fig. 170*D*), situated somewhat dorsally on the eighth abdominal segment, are small and crescent-shaped and have about 12 openings. The anterior spiracles, at the posterior margin of the first thoracic segment, are of similar form but less heavily sclerotized. The larvae of other species are of similar form. That of *S. oreas* O.S. is stated to have the anterior spiracles of elliptical form and situated between the second and third thoracic segments, whereas the posterior spiracles are semicircular, with 9 to 10 openings. In *B. pumilis*, the latter are said to be fan-shaped. In *Cyrtomorpha flaviscutellaris* Rob. (Fuller, 1938), the anterior spiracles are larger than the posterior pair and have five slits whereas the latter has only three, situated at one end of the oval plate. Both pairs of spiracles are completely concealed by folds of the integument. Each of the first seven abdominal segments has a pair of spiracles of minute size.

The pupae of the Bombyliidae are of the free type (Fig. 171) and bear a considerable resemblance to those of the Asilidae, Nemestrinidae, and related forms. One of

the most conspicuous characters is the head crown which consists usually of three pairs of heavily sclerotized, pointed projections, or teeth, of which the medium pair may be bifurcate or otherwise modified. The posterior pair occurs on the proboscis sheath and are close together. In some species, such as *A. anale* Say (Shelford, 1913), the median and anterior pairs are fused at the base to form a fan-shaped crown. Each abdominal segment bears a transverse ring of long slender hairs, and dorsally there is a transverse row of short, curved hooks. The last abdominal segment terminates in one or two pairs of short heavy spines.

Several species lack the conspicuous head crown of spines or teeth described above, among these being *Systropus conopoides* (Kunckel d'Herculais, 1905) which bears instead a pointed plate over the front of the head, markedly similar in form to that

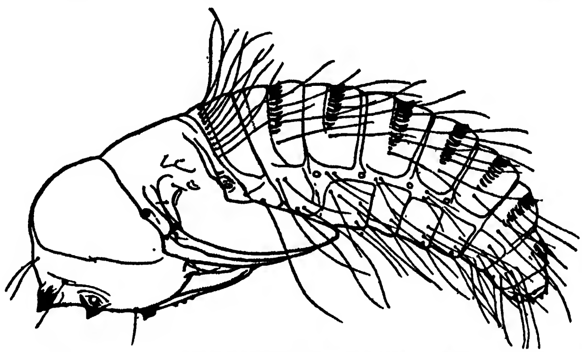


FIG. 171.—The pupa of *Thyridanthrax argentifrons* Austen. (*From Austen.*)

borne by the pupa of its eucleid host, *Sibine bonaerensis* Berg., and which serves the same purpose.

EMPIDIDAE

The so-called dance flies, which constitute this family, are all of small size and found most abundantly in moist places, the larvae occurring principally in soil or decaying wood. The adult flies are all predaceous upon other insects of small size, and the larvae are either predaceous or scavengerous. Whitfield (1925) reports the complete control of an infestation of *Phytomyza aconiti* Hendel through the attack of *Tachydromia minuta* Meig. upon the adult flies. Lundbeck (1910) calls attention to a very unusual feeding habit associated with mating in the genera *Rhampomyia, Empis,* and *Hilara.* The male captures a victim and carries it about until mating takes place, whereupon it is transferred to the female. The males of several species envelop the prey in a frothy web before presenting it to the female.

DOLICHOPODIDAE

The adults of this family of long-legged flies are all predaceous upon other insects and lower forms of animal life of suitable size. Many species are found in swampy areas and along muddy shores, and the adults of some forms are capable of running over the surface of the water. The

females move very rapidly and often have a crab-like manner of locomotion. Williams (1933) mentions that the adults of several species of *Campsicnemus* are very active upon the surface of water pools in Hawaii and that they feed extensively upon the collembolan, *Salina maculata* Fols. He also observed the adults of *Hydrophorus pacificus* V.D. pulling *Chironomus* larvae out of shallow water along muddy shores and in marshes.

Detailed information regarding the predaceous habits of the larvae is limited to the genus *Medetera*, the hosts of which are mainly the larvae, pupae, and adults of bark beetles. A short account of the habits of *M. signaticornis* Lw., predaceous upon larvae and adults of Scolytidae, is given by Hubault (1925); and a more extended study of *M. aldrichii* Wh. has recently been presented by De Leon (1935*a*). The latter species is an important enemy of the mountain pine beetle, *Dendroctonus monticolae* Hopk. in western North America. The eggs are laid beneath bark scales or in crevices, and the young larvae work their way into the inner bark in search of the immature stages of the host. They also feed upon dead larvae and various other insects that may be found in the burrows. Pupation takes place in a cell in the bark, and this is lined with a silk-like material.

The larvae of a few species of the family are aquatic in habit and feed upon a variety of aquatic animal life. Some are found in moist sand or soil.

MISCELLANEOUS ORTHORRHAPHA

The families Limnobiidae, Blepharoceridae, and Orphnephilidae are largely or entirely aquatic in habit, and the larvae feed in part upon minute organisms such as diatoms and upon small Crustacea. The adults of the Blepharoceridae feed extensively upon midges and other small, soft-bodied insects.

CYCLORRHAPHA

PHORIDAE

These minute flies, of which some species are wingless, have a distinctly humpbacked appearance, due to the large thorax, the small head, and the tapering abdomen, which is usually directed somewhat ventrad. They move very quickly and in a characteristic jerky manner. Many of the parasitic species are distinguished by the possession of a long, heavily chitinized ovipositor.

FOOD AND HOST PREFERENCES

These flies are often found abundantly in the vicinity of decaying vegetation, and probably the great majority of species are scavengers,

some feeding upon vegetable matter including fungi, many upon decomposing insects, snails, etc., and others upon carrion. Larvae and pupae of a number of species have been taken from mole nests. The myrmecophilous and termitophilous genera and species include the more degraded representatives of the family; they are either scavengers or commensals.

The entomophagous species of which the food preferences are known exhibit a wide diversity in hosts. A number of species are parasitic in ants, principally the adults, though the pupae also are subject to attack. Other parasitic species develop in coccinellid pupae, lepi-

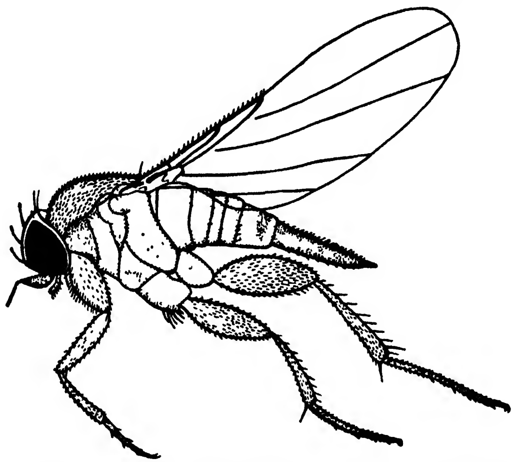


FIG. 172.—The adult female of *Melaloncha pulchella* Brues. (*Redrawn, after Brues*, 1903.)

dopterous larvae and pupae, dipterous larvae, adult bees and crickets, and myriapods. Those of predaceous rather than parasitic habit develop upon the eggs of spiders and locusts. A single species, *Syneura cocciphila* Coq., of South America and the West Indies, attacks those of the cottony-cushion scale, *Icerya purchasi* Mask. Several species have been taken from the egg cases of *Locusta migratoria* L.

Malloch (1912) has given a complete record of the food and host preferences known for the family at that time. In many cases, the association of species with other insects or lower animals has been definitely established, but the exact relationship remains obscure. Very evidently the line between the scavengerous and parasitic habits is not distinct; a species may develop in either way, or it may attack living organisms that, while still living, are in an unhealthy condition or are wounded and will soon die. Accordingly, a species can seldom be considered as parasitic in the absence of experimental proof, consisting of demonstrated oviposition upon or in healthy hosts and the attainment of maturity by the progeny.

From the economic point of view, the entomophagous Phoridae must be classed as predominantly injurious rather than beneficial. This is due to their quite general attack upon coccinellid pupae, adult bees, and spider eggs. The one distinctly beneficial species is *S. cocciphila*, a common enemy of the cottony-cushion scale.

BIOLOGY AND HABITS

Among the parasitic species of the family, one of the best known is *Megaselia fasciata* Fall., a gregarious internal parasite of the pupae of many genera of Coccinellidae in Europe, which has been studied by Lichtenstein (1920) and Menozzi (1927). The number of individuals developing in each host is, of course, dependent upon the size, but 8 to 14 reach maturity in each pupa of *Coccinella*. The parasite may at times act as an important check upon the increase of these beneficial beetles, as shown by the fact that a parasitization of 48 per cent has been noted upon *Adalia*. In oviposition, the female stands transversely upon the thorax of the freshly formed pupa and curves the ovipositor beneath it, and the eggs are deposited externally in small clusters between the legs. In some instances, eggs are also deposited upon the bodies of larvae that are approaching the time for pupation. Embryonic development is well-advanced at the time of oviposition, and hatching may take place within three hours. Lichtenstein, however, states that external incubation requires 1.5 to 2.6 days. The eggshells fall from the host very soon after hatching, and consequently there is no external evidence of attack. The newly hatched larvae immediately penetrate the body at the base of one of the legs, and their ensuing development is very rapid. Feeding is completed in 2 to 5 days, and the larvae then emerge through an opening between the head and thorax and enter the soil for pupation. Parasitized pupae retain their normal form, though at death they assume an erect position which is in contrast to the horizontal position of healthy individuals.

The female flies feed upon the body fluids exuding from punctures made with the ovipositor; this habit may be closely associated with oviposition.

M. aletiae Comst. has been reared from the larvae and pupae of several species of Lepidoptera, but there has been a considerable difference of opinion as to the true relationship. Balduf (1928*a*) states that oviposition upon *Achatodes zeae* Harr. usually takes place only when the larvae are diseased or feeble, and the species is consequently more of a scavenger than a parasite. This conclusion is borne out by the manner in which the larvae enter the body. They do so through the anal opening rather than by penetrating the integument. The mass of larvae that develop causes the posterior third of the host body to be

appreciably distended. Entry is effected into the body cavity, and the store of adipose tissue is the principal source of food. The larval stage is complete in 11 to 15 days, and pupation takes place in the host tunnel.

Timon-David (1938) contributes an interesting note regarding *M. giraudii* Egger as a parasite of a grasshopper, *Phasgoneura viridissima* L. in Europe. An adult host, fully active at the time of capture, later yielded a dozen mature maggots of *Megaselia.* These emerged from a large opening in the integument at the side of the mesothorax. Dissection of the host remains revealed that the muscular tissue of the thorax had been completely eaten away.

Several species of *Megaselia* are known to be parasitic upon myriapods. *M. juli* Brues was the first species noted to have this habit, and Myers (1934) observed several instances of groups of females persistently attacking live individuals, this continuing in each case for several hours. The hosts make strenuous efforts to ward off the attack, but in vain. The flies always approach with the ovipositors extended and center their attention in the head region. Larval development is complete in about three days, and the body contents of the host are completely consumed by the mass of maggots.

Picard (1930) observed *M. cuspidata* Schmitz attacking a European myriapod, *Iulus sabulosus* L., and came to the conclusion that oviposition takes place in minute wounds in the integument. The species is a true parasite, however, for these wounds, in themselves, would not result in death. Berland (1933), in commenting upon the habits of Phoridae attacking ants and myriapods, expresses the opinion that the larvae are able to gain entry to the body cavity of the host only through wounds.

Hypocera incrassata Meig. is recorded as a solitary internal parasite of the larva of a bibionid fly, *Bibio marci* L., in England (Morris, 1922). The mature larva emerges from the dead body of the host and pupates in the soil. The solitary habit is rare in this family.

The habits of *Melaloncha ronnai* Borgm. (Ronna, 1936, '37) are of particular interest because of the serious losses that it inflicts in apiaries in Brazil through its attack upon the adult bees. A mortality up to 50 per cent has been observed, the higher figures usually being found in apiaries situated in shaded and damp places. The female deposits her egg in the abdomen of the bee. The young larva causes an appreciable displacement of the abdominal organs but apparently produces no serious injury. It soon migrates into the thorax, where it feeds upon the muscular tissues and quickly attains maturity. Parasitized bees experience difficulty in flight and finally fall to the ground, walk about irregularly for a time, and die. The tissues of the thorax are almost entirely eaten away, and the head and prothorax of the bee become detached from the remainder of the body or remain connected with it only at one

side. Pupation takes place most frequently within the thorax of the dead bee, with the anterior end of the puparium exposed. This species is generally solitary in habit, though occasionally two individuals attain maturity in a single host. The egg and larval periods are completed in about 10 days, and the adult fly emerges three to four weeks later. For control, the author suggests the use of glass traps containing a soap solution in which dead bees have been placed. This decomposing mass is said to be very attractive to the *Melaloncha* adults.

Many species of Phoridae are associated with ants in various capacities, but only those of parasitic habit will be dealt with here. The parasitic species are included in a considerable number of genera, of which *Plastophora* is most frequently encountered. Borgmeier (1928, '31) lists the species of five genera known to parasitize ants of the genus *Atta* and related forms, and an additional genus has recently been described by Greene from North America. All these are characterized by a pronounced development of the ovipositor, this being extreme in *Myrmosicorius*.

Apocephalus pergandei Coq. is a solitary internal parasite of the workers of the carpenter ant, *Camponotus pennsylvanicus* De G. (Pergande, 1901). The female fly pounces upon the ant in the open and deposits the egg upon the head, and the young larva then enters through the occipital foramen. Feeding is limited to the contents of the head, which is finally completely hollowed out and detached from the remainder of the body. Pupation also takes place within the head cavity. This is very evidently the species previously observed by Fox (1888), for the host species and larval habits are identical. The adult fly was not secured, and consequently the species could not be identified.

Malloch records the rearing by Pergande of *Megaselia conica* Malloch from the abdomen of *C. pennsylvanicus*, but no details are given regarding the manner of attack.

The most extended observations upon *Plastophora* are those by Wasmann (1918), who describes the association of *P. formicarium* Verr. with *Lasius* spp. It is also recorded as attacking *Myrmica* and other genera in various parts of Europe. The adult flies hover over the ant nest, or at any points where the ants congregate, and are evidently strongly attracted by their odor. Fifty or sixty individuals were seen about a single nest. Rather curiously, only the worker ants are attacked, the winged males and females being ignored. Likewise, dead or injured ants lose their attractiveness, and the species is consequently not a scavenger. The female pounces upon the worker from the air, and the latter makes a determined effort to escape or to defend itself. After alighting, the parasite persistently follows in the rear of the ant, always centering her attention on the abdomen. Finally, she pounces upon

her victim and presumably inserts the ovipositor dorsally between the abdominal segments. There was no indication of the deposition of an egg or a larva externally.

M. R. Smith (1928) has observed the attack of *P. crawfordi* Coq. and *P. spatulata* Malloch upon the fire ant, *Solenopsis geminata* F., in Mississippi. In these species, also, attack is restricted to the workers. The female strikes the ant from above with great rapidity, apparently in the anterior portion of the body. The victim falls upon its side and is apparently stunned or paralyzed for several seconds. It is assumed that these species are parasitic, but none has yet been reared from this host. Fage (1933) reports almost identical habits in *Plastophora* sp. attacking *Camponotus* in Europe.

FIG. 173.—Puparia of *Syneura cocciphila* Coq. in an egg sac of *Icerya purchasi* Mask. (*From Fonseca and Autuori*, 1938.)

The parasitic relationship between *Plastophora* and ants has been taken for granted by various observers, and *P. formicarium* particularly has received considerable attention. The activities of the female flies and the form of the ovipositor certainly lead to the assumption that their attack is for purposes of oviposition directly into the body of the worker ants. The fact remains, however, that no proof of this has yet been presented. The larvae have not yet been taken from the bodies of ants, nor have the pupae been found under conditions that would definitely establish this relationship.

The number of Phoridae of predaceous habit is relatively small, and those which are known develop upon the eggs of other insects and spiders. The species of *Termitoxenia* are said to feed upon the eggs of termites, while Malloch records *Megaselia epeirae* Brues as reared from the egg sacs of spiders. In Japan, an undetermined species was found in a very large portion of the egg sacs observed, some containing up to 200 to 300 larvae and puparia.

Observations upon the biology and habits of *Syneura cocciphila* Coq. (*infraposita* B.S.) have been recorded by Autuori (1928) and Fonseca and Autuori (1938). In the first publication, this species was stated to be a gregarious internal parasite of the adult females of *Icerya*, but this was later found to be erroneous and its true status as an egg and larval predator established. A maximum of 55 individuals may develop to matur-

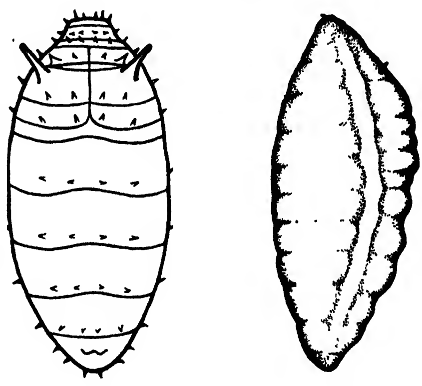
ity upon the contents of one egg sac. Though feeding is largely upon the eggs, yet the maggots also attack the young larvae during the time they remain within the sac. Larval development is rapid, and pupation takes place mainly inside the sac (Fig. 173). No other hosts of this species are known in Brazil or the West Indies, but these must occur, considering that *I. purchasi* is a relatively recent introduction into the Western Hemisphere.

IMMATURE STAGES

It is proposed to give here not a detailed description of the immature stages of the family but only the general characters by means of which the parasitic and predaceous forms may be distinguished from other Diptera that may attack the same hosts.

The eggs of very few species are known. These are of simple form and several times longer than wide, the anterior end wider than the posterior and both smoothly rounded, with the chorion white and smooth.

The first-instar larva lacks the anterior spiracles. The mature larva of *Hypocera incrassata* is rather elongate in form and, like many other parasite species, differs from those which develop as scavengers in the absence or great reduction of the numerous sensory spines and fleshy processes upon the cuticle of the body segments. This distinction, however, does not apply in all cases. The body segments of *Hypocera* are fairly distinct, though somewhat obscured by supplementary folds. The buccopharyngeal armature is of three parts, with the mandibular sclerite in the form of a single stout structure. The anterior and posterior spiracles are almost identical, are slightly elevated, and have four oval openings. The larva of *S. cocciphila* is more robust in form and bears a transverse row of small setae dorsally and laterally on each body segment. In *Melaloncha ronnai*, the body segments bear a fine pubescence and a varying number of long, slender fleshy processes dorsally and laterally. The posterior spiracles are simple and circular in form. In most species of the family, these have four openings, whereas the anterior spiracles have only two. For a detailed study of the morphology of phorid larvae, the reader is referred to Keilin (1911*a*), who describes the larvae of several scavengerous species.



A *B*

FIG. 174.—*A*, The puparium of *Syneura cocciphila* Coq., dorsal view (*from Autuori*, 1928); *B*, the same of *Hypocera incrassata* Meig. (*from Morris*, 1922).

The puparia of this family are readily recognizable because of their distinctive form (Fig. 174). Instead of being circular in transverse section, the lateral margins are flattened dorsoventrally. The greatest thickness occurs in the third or fourth abdominal segments, and the preceding thoracic and abdominal segments taper sharply. The dorsum is much less convex than the ventral side of the body, and this, with the distinct lateral margins, gives the puparium a boat-like appearance. In some species, such as *M. ronnai*, the puparium in lateral view is somewhat S-shaped, owing to the depression of the dorsum of the abdomen, the concavity of the anterior ventral area, and the marked convexity of the ventral surface of the abdomen. The

prothoracic cornicles of the pupa project from the anterior margin of the second thoracic segment; they may be small, or they may equal several segments in length.

In some species, emergence from the puparium is effected by forcing off the operculum, consisting of the dorsal portion of the first and second and most of the third thoracic segments, in a single piece; in other species, the operculum splits into two parts along the median line.

PIPUNCULIDAE

The flies of this family, of which *Pipunculus* is the dominant genus, are readily recognized by the unusually large head and the enormous

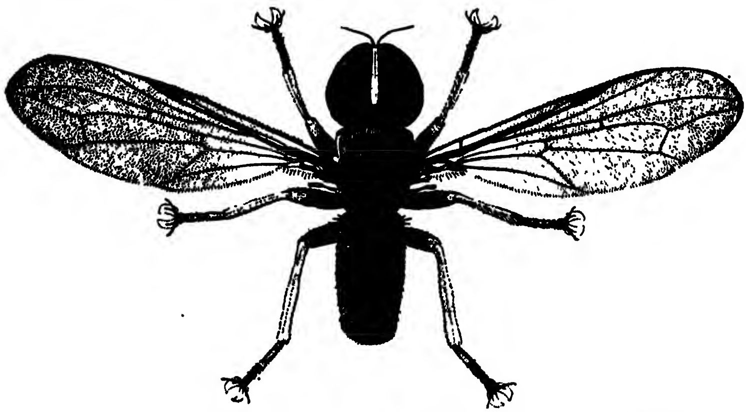


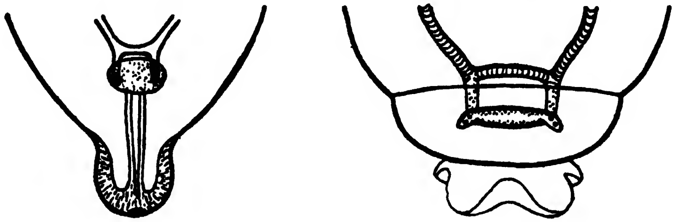
FIG. 175.—The adult female of *Pipunculus cruciator* Perk. (*From Perkins*, 1905.)

eyes. So far as known, all species are solitary internal parasites of the nymphs and adults of various Homoptera, particularly the Cicadellidae, Cercopidae, and Delphacidae. No complete study has been made of the biology and habits of any species, though information is given regarding certain of the immature stages of *Pipunculus* sp. by Perkins (1905*e*) and of *Ateleneura spuria* Meig. by Keilin and Thompson (1915*a*).

The few observations that have been made upon the manner of oviposition indicate that the female fly pounces upon the host nymph while the latter is feeding or resting upon the foliage and that it is then carried into the air; meanwhile, the abdomen of the parasite is curved beneath the body and the ovipositor inserted through the intersegmental membrane of the abdomen. Presumably, the egg lies free in the body cavity, though this has not been definitely determined, nor has the egg of any species been described. There appears to be no proof for the assertion by several authors that oviposition in some species is external and that the young larva makes its own way into the host body. The structure of the ovipositor of the females of the family is distinctly of the piercing type.

Keilin and Thompson record only two larval instars of *A. spuria*, the second having all the characteristics of a normal cyclorrhaphous larva

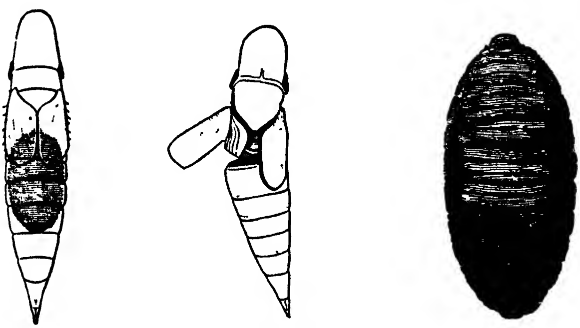
of the third instar. The first instar is 1.0 mm. in length and somewhat elongate and bears a vesicle-like organ at the posterior end of the body. The skin bears no sensory spines or setae, and no tracheal system is distinguishable until late in the stage, when the lateral trunks become filled with air. The second-instar (Fig. 176*A*), or mature, larva is robust



A *B*

FIG. 176.—*A*, the posterior portion of a second-instar larva of *Ateleneura spuria* Meig. (*from Keilin and Thompson*, 1917); *B*, that of a third-instar pipunculid larva, showing the spiracular plate and the anal vesicle (*from de Meijere*, 1917).

and oval in outline, with the caudal vesicle still present though relatively reduced in size. The anterior spiracles are elevated, and each has four to five openings. The posterior spiracles, each of which has three openings, are also elevated and are situated at the lateral margins of a large, black, heavily sclerotized peristigmatic plate. This single plate, upon which both spiracles are borne, is characteristic of the family.



A *B* *C*

FIG. 177.—*A*, a nymph of *Hecalus* sp. containing a larva of *Pipunculus cruciator* Perk.: *B*, the same after the emergence of the *Pipunculus* larva; *C*, a mature larva of *P. javator* Perk. (*From Perkins*, 1905.)

Almost invariably the advanced first-instar *Ateleneura* larva lies with its head directed toward the thorax of the host, whereas after the molt the position is reversed, the head being near the tip of the abdomen and the caudal extremity at the juncture of the abdomen and thorax. Parasitized leaf hoppers containing nearly mature *Pipunculus* larvae may be readily recognized by the distended condition of the abdomen. The

larva emerges from the *Typhlocyba* nymph or adult through an opening made between two segments of the abdomen and enters the soil for pupation.

In *Pipunculus* sp. studied by Perkins, the larvae were always found to lie with the head directed cephalad, and emergence was through an opening at the juncture of the thorax and abdomen (Fig. 177). In *P. xanthocnemis* Perk., parasitic in *Liburnia*, the emergence hole is in the

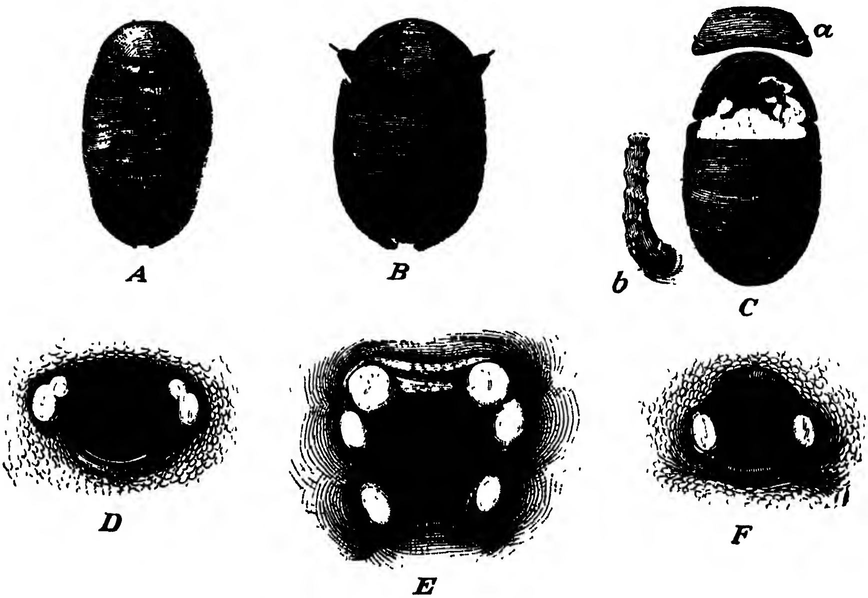


FIG. 178.—Puparia of the Pipunculidae. *A*, the common form of the family; *B*, ***Pipunculus cinerascens*** **Perk.**; *C*, an empty puparium of *P. koebelei* Perk., showing the operculum and a pupal prothoracic cornicle; *D*, the posterior spiracular area of *P. cruciator* Perk.; *E*, the same of *P. cinerascens*; *F*, the same of *P. hylaeus* Perk. (*From Perkins*, 1905.)

mid-dorsal area of the abdomen. Subramaniam (1922) mentions that the mature larvae of *P. annulifemur* Brun. have a habit of jumping, after the manner of fruit-fly larvae. Although the majority of species pupate in the soil, yet some, like *P. cinerascens* Perk., form their puparia upon the foliage. The larva of *P. xanthocerus* Kow. differs from others of the family in having the integument heavily spinose rather than smooth, and this character persists in the puparium.

The puparia of the Pipunculidae are broadly oblong in outline, often with a granular or rugulose sculpturing, and are red, brown, or black in color. In some species, the prothoracic cornicles are exceedingly minute and can barely be seen projecting through the puparial wall, whereas in other species, such as *P. cinerascens* (Fig. 178*B*), they are borne at the apices of very large conical processes. The posterior stigmatic area is

rounded in some species and depressed in others, with the spiracles borne at the lateral margins. Usually, each spiracle has three openings, though in some species there are two and in others only one (Fig. 178*D* to *F*). At the time of emergence of the fly, the entire anterior portion of the puparium is completely or partly forced off in two parts, the dorsal one usually bearing the prothoracic cornicles. The transverse line of fracture is slightly behind the anterior margin of the second abdominal segment.

With respect to *Chalarus* and *Verallia*, Lundbeck (1922) calls attention to a modification in the manner of emergence from the puparium. The two anterior plates, which are forced off, are broken further, the upper one

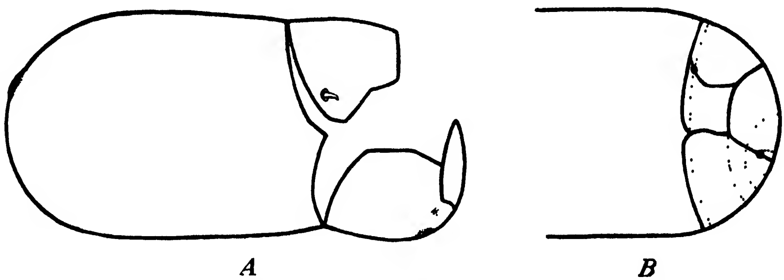


FIG. 179.—*A*, Outline of a pipunculid puparium, showing the lines of fracture; *B*, a lateral outline sketch, somewhat diagrammatic, showing the relationship of the five parts of the operculum to the segmental lines. (*Redrawn, after de Meijere*, 1917.)

into three parts and the lower into two. Thus, five pieces are detached from the puparium as compared with two in *Pipunculus*. The prothoracic cornicles occur along the line of fracture and are not a part of the median dorsal plate. The relation between the five parts and the lines of fracture are shown by De Meijere (1917) for an undetermined species of the family (Fig. 179).

The duration of the life cycle is known only for the several species of *Pipunculus* established in Hawaii (Swezey, 1936), in which the combined egg and larval stages cover 40 days and the pupal stage about one month. In *P. annulifemur*, the pupal stage is completed in 14 to 19 days.

SYRPHIDAE

The species of this large and well-known family exhibit a considerable range in habit, some being aquatic and feeding upon decaying animal and vegetable matter and others occurring in decaying wood. The genus *Microdon* is found in the nests of ants, presumably in a commensal capacity. *Volucella* lives as a scavenger in the nests of bumblebees and wasps. A few species, particularly of the genera *Mesogramma*, *Merodon*, and *Eumerus*, are phytophagous, and species of several genera develop in the sap exuding from wounds in trees. The great majority, however, are

predaceous upon aphids, though a small number attack Chermidae, dactylopine Coccidae, Cercopidae, and lepidopterous larvae.

The species having predaceous larvae represent a considerable number of genera, and there is little variation in habit among them. Campbell and Davidson (1924) have presented studies upon the food habits of a number of aphid-feeding species occurring in California. The eggs are usually deposited singly on the leaf or bark surface among the aphid and mealybug colonies. Incomplete information indicates that the females are capable of depositing several hundred eggs, with a maximum for one day of about twenty-five. Feeding experiments reveal that up to 400

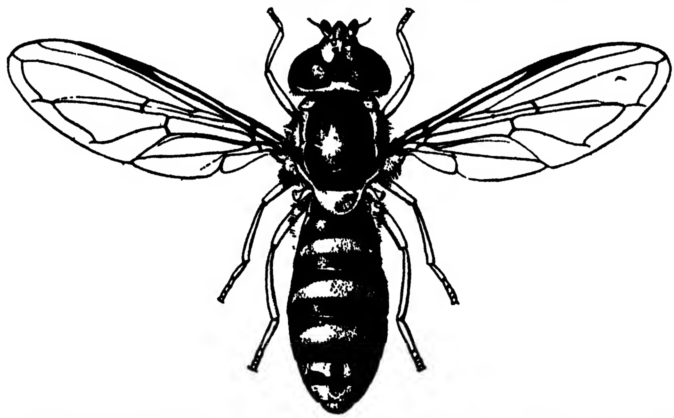


FIG. 180.—The adult female of *Sphaerophoria cylindrica* Say. (*From Webster and Phillips*, 1912.)

aphids are consumed by a single larva during its development, the number, of course, varying with the size of the species and the stage and species of host provided. Several species were able to complete their development upon 100 or fewer first- to fourth-instar aphids. A scarcity of food material results in the prolongation of the larval stage. Metcalf (1917) has given an extended account of the biology of several aphid-feeding species occurring in the northeastern United States.

Salpingogaster nigra Sch. is a common enemy of the sugarcane froghopper, *Tomaspis saccharina* Dist., in the British West Indies (Guppy, 1913, '14). The eggs are deposited in small clusters directly into the spittle mass of the host and hatch in 2 to 3 days. Larval development is completed in 9 to 10 days, and during this period a total of 30 to 40 froghopper nymphs are destroyed. In attacking the host, the maggot usually pierces it dorsally behind the first abdominal segment. The pupal stage covers 9 days, and the species is thus able to produce successive generations at less than one-month intervals so long as moisture conditions are satisfactory. In Trinidad, the biological control of the froghopper has been attempted by means of this predator.

In New Zealand, the larvae of *Syrphus rapalus* Wlk. (Miller and Watt, 1915) are well-adapted for attack on the caterpillars of *Venusa verriculata* on the foliage of cabbage trees. The latter congregate on the inner surface of the outer leaves which enclose the heart spike and the *Syrphus* larvae, being negatively phototropic, favor the same location. In Europe, *Xanthandrus comptus* Harr. has been noted to feed upon the larvae of *Pieris brassicae* L., *Cnethocampa pinivora* Tr., etc., and it appears to be a common predator upon various caterpillars. H. D. Smith (1936) records his observations upon 12 colonies of *Cnethocampa*, the well-known processionary caterpillar, in France, and found that *Xanthandrus* larvae were present in practically all of them. The population of 11 of the 12 colonies had been largely or entirely destroyed. An average of 2.5 larvae were found in each nest. In one colony containing 80 caterpillars, probably of the first instar, all had been killed. An exceptional range in host preferences is shown by this species which, in addition to preying upon various caterpillars, is stated to be more generally an aphid predator. In some species, the larvae pupate among the host colonies upon the foliage, whereas in others they descend to the ground and form the puparia among the rubbish.

The life cycles of the aphid- and mealybug-feeding species are of fairly uniform duration and cover a period of 16 to 28 days from deposition of the egg to the emergence of the adult. Incubation of the egg requires 2 to 3 days at summer temperatures, and the larval and pupal stages are of approximately equal length. There are five to seven generations each year, and the winter is passed in the pupal stage. *S. rapalus* is a striking exception, in that the larval period covers several months.

Kamal (1939) calls attention to a pronounced tendency toward migration on the part of the mature larvae, this being induced by the need for moist surroundings for pupation. In an aphid infested alfalfa field in California, he noted a marked scarcity of mature larvae and puparia, and a search revealed that vast numbers of larvae had moved to the field margins and pupated in the damp soil along ditch embankments, some having penetrated to a depth of 10 to 15 cm. In particularly favored spots, the puparia were massed in great numbers.

IMMATURE STAGES

The eggs of the entomophagous representatives of the family are quite similar in form and appearance, being subcylindrical, about 1 mm. in length, one-fourth as wide as long, and slightly arched, with a small conical micropyle. The surface bears a waxy covering which ranges in color from a glistening white to grayish-white, with fine reticulations or longitudinal ridges, most frequently the latter.

Heiss (1938) has given an extended account of the classification of the larvae and pupae of the family, exclusive of the aquatic forms. Characters and keys are given by means of which the various genera can be distinguished. An outstanding contribution to the biology, morphology, and anatomy of the larvae of a series of aphidophagous

species has recently been presented by M. L. Bhatia (1939). The reader is referred to these two papers for a detailed discussion of the characters of the larvae and pupae, which will be described here only in very general terms.

The three larval instars are slug-like in general appearance, and those of the entomophagous species are very similar in form. The larvae are distinguished from those of other cyclorrhaphous families by two characters: (1) The posterior respiratory tubes of the second and third instars are contiguous and partly or completely fused. (2) Each body segment bears 12 spines, in definite positions. Prolegs are lacking, whereas they occur frequently among the saprophytic species. The body usually tapers anteriorly, and the body contents are distinctly visible through the thin integument. The anterior spiracles are relatively small, whereas the posterior spiracles of the mature larvae (Fig. 181) are large, contiguous or nearly so, and often situated at the tip of a single heavy stalk. They bear three slits which, among the different species, vary in position and direction with respect to the spiracular button. Many if not all representatives of this family possess so-called rectal gills, which are rarely found extruded in the entomophagous forms. Each gill consists of a pair of simple finger-like processes joined at the base.

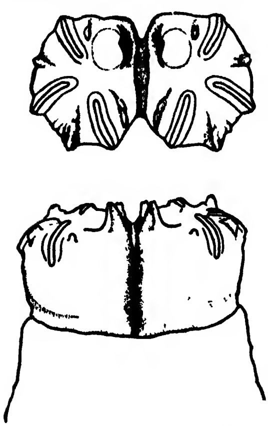


FIG. 181.—The posterior spiracles of the mature larva of *Syrphus knabi* Shannon. (*From Heiss*, 1938.)

The body color and markings are typical for each species, the former usually being due not to pigmentation of the integument but to coloring matter contained in the fat bodies, the arrangement of which also differs among species. There is likewise a variation in color of the body fluids, which is often due to the food consumed by the larvae.

The puparium (Fig. 182) consists of the indurated exuviae of the third-instar larva and is of tear-drop form with the posterior segments markedly narrowed and the anterior portion broadly rounded. The integumentary spines and processes of the larvae of the species that bear such ornamentation are shrunken and distorted. The prothoracic cornicles of the pupa do not protrude through the puparial wall, and the minute anterior spiracles of the larva are almost invisible. The operculum is circular and divided transversely into a dorsal and a ventral piece, which separate upon emergence of the adult.

FIG. 182.—The puparium of *Baccha siphanticida* Terry. (*From Terry*, 1905.)

CONOPIDAE

The members of this family, comprising the large-headed flies, are relatively few in number of genera and species. Many of the adults have a superficial resemblance to Syrphidae. The females of a number of species have the caudal segments of the abdomen modified ventrally into a pincer-like form, which may be an adaptation, similar to that found in some Tachinidae, for grasping the host at the time of oviposition. Other species, such as those of the genus *Stylogaster*, have long, slender ovipositors.

HOST PREFERENCES

The Conopidae are predominantly solitary internal parasites of adult bumblebees, though a number of species have been reared from various Sphecoidea and Vespoidea, particularly of the genus *Vespa*. The observations that have been made upon the host preferences of the genus *Stylogaster*, which is associated with ants in the tropics, have been reviewed by Aldrich (1930). Some authors express the opinion that the flies oviposit in the ants themselves or in other insects driven from their hiding places by the ants, that they are predaceous upon the larvae, etc. None has ever been reared, but it is pointed out that parasitic development in the adult ants themselves is improbable because of the fly being of much greater size than the ants. Silvestri (1926) records the finding of a larva, believed to be a conopid, in the head of a *Termes gilvus* Hag. worker in the Philippine Islands. There is some evidence to indicate that certain species are parasitic in Acrididae.

Owing to their comparative scarcity, the Conopidae are of very little economic importance except in so far as their attack upon bumblebees may reduce blossom pollination. Severin (1937) has called attention to *Zodion fulvifrons* Say as a parasite of worker honeybees in South Dakota and states that it causes heavy losses at certain times.

BIOLOGY AND HABITS

The early information on biology and habits of the Conopidae was summarized by Saunders in 1858, who gave also his own observations upon the habits of *Physocephala flavipes* L. and described and figured the mature larva and puparium. He calls attention to the conclusions of Robineau-Desvoidy and Dufour early in the nineteenth century that these flies ovipost directly into the adult hymenopterous hosts. Several later authors believed that the eggs were deposited externally upon them, but none was able to observe the eggs upon the body or the eggshells upon hosts from which larvae were taken. Even more recently, other writers have asserted that the species attacking *Vespa* oviposit in the larvae in the nest and that maturity is reached when the host becomes adult. No direct evidence has been brought forward to support this conclusion. Pantel's (1910) studies upon the reproductive system of the females convinced him that oviposition is internal, and the extended studies by De Meijere (1904, '12) upon a number of European species confirm this conclusion and prove that it takes place in the adult host. The eggs show no embryonic development at the time of deposition. To the latter author is owing the greater part of our present knowledge regarding the early stages and habits of the family.

In the majority of species in which the oviposition habit has been observed, the female pounces upon the host and oviposits while the latter is in flight. The contact is only momentary, however; and if the egg is deposited at this time, the insertion of the ovipositor must be exceedingly rapid. There is no struggle between parasite and host such as occurs during oviposition by the Pyrgotidae. The above manner of attack has been noted in *P. rufipes* F. and *P. tibialis* Say, which are parasitic on bumblebees in Europe. The females of *Conops scutellatus*

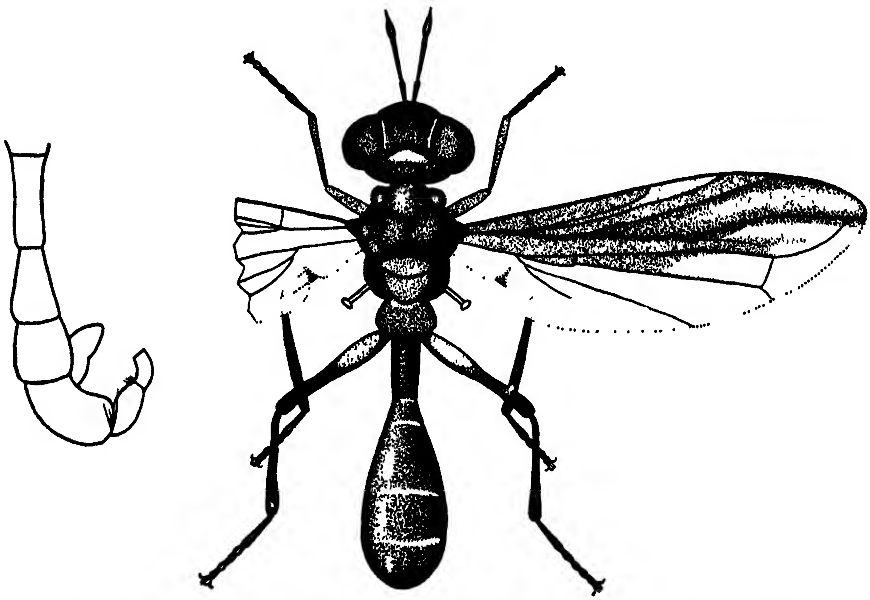


FIG. 183.—The adult female of *Physocephala carbonaria* Will., with outline of lateral view of the abdomen. (*Redrawn, after Williston*, 1892.)

Meig. congregate in some numbers about the entrances of *Vespa* nests and pounce upon the wasps as they enter. In a number of instances of species known to parasitize nest-building wasps and bees, the females have been seen actually to enter the nests, though it is not known that oviposition takes place therein. The fact that some colonies show an exceptionally high parasitization lends some support to the belief that this does occur. The workers of the social wasps are most generally attacked, though the males and females are not immune.

Very little information is available regarding the development of the early stages. The first- and second-instar larvae apparently lie free in the abdominal cavity and absorb their food from the blood of the host. More extensive feeding takes place in the third stage, and all the contents of the abdomen are consumed. Several investigators have recorded

collection of bees feeding at blossoms which, upon examination, were found to contain third-instar conopid larvae. At no time do these larvae enter the thorax, and the absence of injury to the muscles in that region accounts for the continued activity of the host until the parasite larva is nearly mature. The second- and third-instar larvae are stated to have their posterior spiracles firmly attached to one of the tracheal air sacs. Death of the host takes place only a short time before the completion of larval feeding, and the dead bees or wasps are usually found in the nest or near the entrance to it. They may often be readily recognized by the swollen condition of the abdomen.

Pupation takes place within the abdomen of the dead host, and the puparium completely fills it. The position in which it is found is quite constant, the body being inverted with respect to the host and the head end at the base of the abdomen. An exception to this rule is *Sicus ferrugineus* L. in which the head is directed toward the caudal end of the abdomen of the host, the change in position having been made by the larva just prior to pupation. Emergence of the adult fly is effected by a rupture of the intersegmental membranes of the host ventrally, usually between the first and second abdominal segments; or if the disintegration of the host body has progressed sufficiently far, the body may be broken in two at that point. At emergence, the anterior portion of the puparium breaks away in two parts, one ventral and the other dorsal, and the posterior line of cleavage of the latter is between the metathoracic and first abdominal segments.

The life cycle has not been determined experimentally for any species, though the evidence indicates that the majority of species have a single generation each year, with some possibly requiring two years. The feeding period is believed to be quite short, probably being complete in about two weeks, and the winter is passed within the puparium in the body of the dead host.

IMMATURE STAGES

The only observations thus far made on the eggs of the Conopidae are by De Meijere, who has described and figured those of several species. The body of the egg is quite large, ranging from 0.7 mm. to 1.4 mm. in length, with the greatest width one-fifth to one-fourth the length. It tapers gradually to a rather blunt point at the posterior end in *Dalmannia punctata* F. (Fig. 184*B*), whereas in *Physocephala flavipes* L. (Fig. 184*C*) the maximum width is near the posterior end and the tip is drawn out to a sharp point. The distinguishing feature among the eggs of the different species of the family is the form and size of the anterior stalk and the micropylar structure. In *D. punctata*, the stalk is small and button-like, with a series of small flanges radiating from the distal end. This egg is quite similar to that of *Adapsilia* in the family Pyrgotidae. In *P. rufipes*, the short stalk bears distally about 20 long, slender tubular processes, each 3 μ in width. *P. flavipes*, *P. vittatus* F., and *Zodion notatum* Meig. have similar modifications with a variation in the length of the stalk and in the number of

the filamentous processes. The eggs of *Myopa buccata* L. (Fig. 184*A*) and *Sicus ferrugineus* are essentially similar to that of *D. punctata*, though with the stalk considerably longer and heavier and terminating in four heavy hook-like flanges. The micropyle is borne at the end of the stalk. The purpose of these flanged micropylar structures is not clear, but they would appear to be admirably suited to fixing the stalk in the oviposition puncture in the intersegmental membrane or to an abdominal air sac of the host, by which means an air supply for the developing embryo would be ensured. The laid egg has been secured only in *S. ferrugineus*, and in this instance it was found free in the abdominal cavity of the host, alongside a trachea.

The first-instar larva has been observed and described only for *P. rufipes* (Fig. 185*A*) and *S. ferrugineus*. The body is distinctly pear-shaped with the greatest width in the mid-abdominal region. The thoracic segments are indistinct, narrow, and elongate, whereas the seven abdominal segments are distinct. The broad caudal

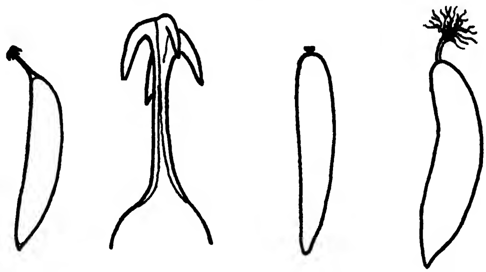


FIG. 184.—Eggs of the Conopidae. *A*, *Myopa buccata* L., with enlargement of the anterior stalk at the right; *B*, *Dalmannia punctata* F.; *C*, *Physocephala flavipes* L. (*From de Meijere*, 1903, '12.)

segment bears two patches of dark spines. Anterior spiracles are lacking, and the posterior pair, which are markedly dorsal in position, are small and simple, represented by a dorsally directed hook, set upon a sclerotized plate, with the opening occurring near the tip. The pharyngeal skeleton is not well-developed.

The second-instar larva is likewise pear-shaped, somewhat flattened dorsoventrally, with the thoracic segments long and narrowed. The caudal segment bears a transverse band of spines or warts, interrupted on the median line in some species, beneath the spiracles. *P. rufipes*, *P. vittatus*, and *Zodion* sp. lack the anterior spiracles, whereas in *S. ferrugineus* they occur as minute black dots, comprising about 12 papillae, but are rudimentary and nonfunctional and connect with the tracheal stalk by a solid thread only. In *P. rufipes*, the posterior spiracles (Fig. 185*D*) are large, oval in form, and pointed dorsally and have about 125 papillae arranged in irregular rows. A large stigmatic scar occurs near the inner margin. Those of *P. vittatus* are oblong, are not pointed dorsally, and have about 75 papillae. Slightly in front of each spiracle is found a dark sclerotized tubercle or process, which is surmounted by five blunt spines. In *S. ferrugineus* (Fig. 185*C*), the spiracles are elongate oviform and pointed at the dorsolateral margin and have only 6 to 8 papillae, arranged in an arc. A pair of small oval eversible anal "vesicles" is present. The larva of *Zodion* sp. also bears the sclerotized processes immediately in front of the posterior spiracles.

The third-instar larva has the same general body form as the preceding instars, with the thoracic segments even more attenuated, and the body as a whole is somewhat broader than thick and is yellowish-white in color. The body is almost covered with minute tubercles or setae, most numerous in the dorsal and caudal regions, and those on the thoracic segments are mostly at the anterior margins and arranged in

transverse rows. The anterior spiracles are lacking in *P. rufipes*, *P. sagittaria* Say, *P. vittatus*, and *Zodion* sp., whereas they are present on the posterior margin of the prothorax in *S. ferrugineus* and are fan-shaped, with about 35 openings. The posterior spiracles are very large, convex, ranging from kidney-shaped to almost hemispherical, brown to dark reddish-brown in color, and quite closely set together. The principal variation among species is in the number and arrangement of the spiracular openings. In *P. rufipes*, these are found in circular groups of 5 to 10, the groups themselves numbering about 70. The stigmatic scar is large and situated near the inner margin. The spiracles of *P. vittatus* are somewhat narrower, with about 40 groups of openings,

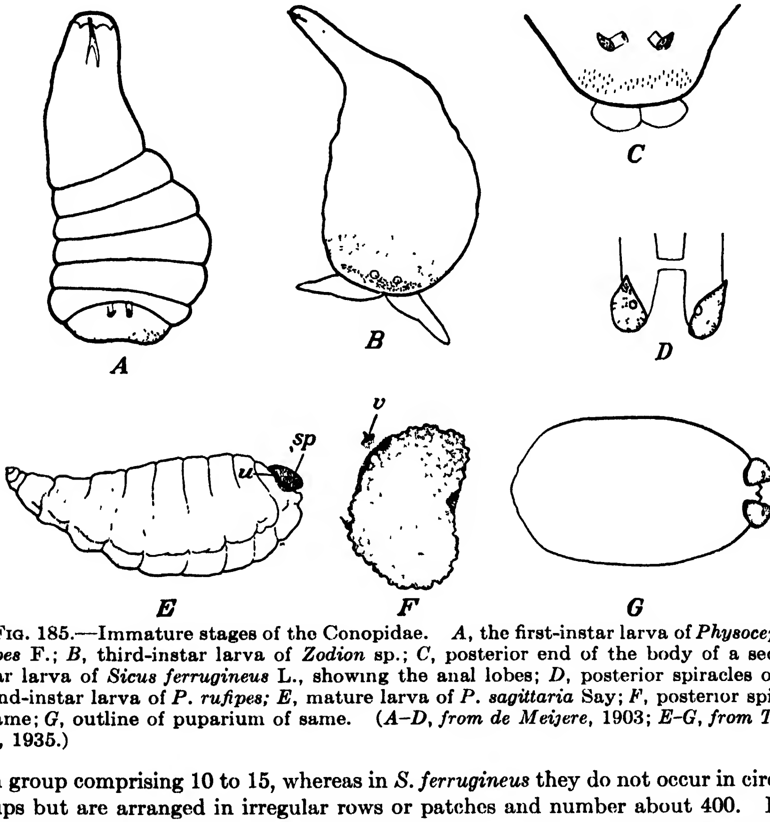


FIG. 185.—Immature stages of the Conopidae. *A*, the first-instar larva of *Physocephala rufipes* F.; *B*, third-instar larva of *Zodion* sp.; *C*, posterior end of the body of a second-instar larva of *Sicus ferrugineus* L., showing the anal lobes; *D*, posterior spiracles of the second-instar larva of *P. rufipes; E*, mature larva of *P. sagittaria* Say; *F*, posterior spiracle of same; *G*, outline of puparium of same. (*A–D, from de Meijere*, 1903; *E–G, from Townsend*, 1935.)

each group comprising 10 to 15, whereas in *S. ferrugineus* they do not occur in circular groups but are arranged in irregular rows or patches and number about 400. In *P. sagittaria* (Townsend, 1935) (Fig. 185*F*) and *Zodion* sp., the groups of openings are situated upon pronounced raised areas. The third-instar larvae of *Zodion* (Fig. 185*B*) and *S. ferrugineus* are also distinguished from those of other species by the presence of a pair of rather large, laterally directed anal vesicles which contain tracheal branches. In all species studied by De Meijere, the small sclerotized process, surmounted by blunt spines, is found dorsally immediately in front of each posterior spiracle. In *P. sagittaria*, it is spine-like in form. These structures may possibly be utilized by the larva in perforating the air sacs of the host so that the spiracles can be applied to the punctures and an air supply thus secured.

A particularly interesting feature in the morphology of the larvae of the Conopidae is the occurrence, in the second and third instars of *S. ferrugineus* and *Zodion* sp., of

the paired anal vesicles, which are retractile. The only other parasitic group of the order known to have a somewhat similar structure is the genus *Cryptochaetum*, of the family Agromyzidae, in which case they are also paired. They differ in origin, however, for those of *Cryptochaetum* are apparently lobes of the body wall. The vesicles of the Conopidae consequently are more nearly homologous with those of various Hymenoptera.

The puparia (Fig. 185*G*) are rather robust in form, not more than twice as long as wide, and somewhat flattened, with the segmentation indistinct and the surface smooth or transversely wrinkled. In *P. rufipes*, the venter is more convex than the dorsum. The anterior end is narrower than the posterior, whereas in certain other species, such as *C. coronatus* Rond., the opposite is true. In color, the puparia are brown to dark reddish-brown, though those of *Z. cinereum* F. are delicate and glossy and have a yellowish-brown or reddish tint. The prothoracic cornicles of the pupa do not protrude through the puparial wall. In *P. rufipes* and *S. ferrugineus*, the prothoracic spiracles are not elevated and comprise up to 115 papillae, arranged in radiating rows. Those of *P. vittatus* are similar but have a smaller number of papillae. The large posterior spiracles are more prominent and project more than in the third-instar larva. De Meijere calls attention to the occurrence of a delicate transparent lining of the puparial wall, which may possibly represent a prepupal exuviae such as has been observed in certain other cyclorrhaphous Diptera.

OTITIDAE (ORTALIDAE)

The members of the family are predominantly plant feeders and are often found as scavengers in decaying plant materials. Lopez (1934), however, has given a brief account of *Elassogaster sepsoides* Wlk. as a predator in the egg capsules of the migratory locust, *Locusta migratoria* var. *migratorioides* R. & F., in the Philippine Islands. This species is considered to be the most important of the natural enemies attacking the eggs of *Locusta* in the islands. Under insectary conditions, maggots were found in the egg capsules within one week after exposure to mated flies. A maximum of 28 maggots was found in one capsule. They are apparently not limited in their feeding to a single mass of eggs but move about in the soil in search of others.

LONCHAEIDAE

The great majority of species of the family develop in decaying vegetation, and only an occasional species is predaceous. According to Taylor (1929, '30), the larvae of *Lonchaea corticis* Taylor are predaceous upon those of *Pissodes strobi* Peck and related beetles, and the species ranks second among the natural enemies of this pest. The eggs are laid in clusters of 6 to 25 in the oviposition burrows of the beetles. The larvae are not restricted entirely to animal food but may also ingest frass, etc. The greatest degree of effectiveness is attained when the hatching of the eggs of both predator and host occur simultaneously, or if that of the former precedes hatching of the host by a few days to one week.

PYRGOTIDAE

The flies of this family are of medium to large size, with long wings, often partly clouded. A relatively small number of genera and species are known, and the host preferences have been determined for only a few species. These are solitary or gregarious internal parasites of adult beetles of the family Scarabaeidae. *Pyrgota undata* Wied. which has been studied by Davis (1919) is nocturnal in habit, as are its hosts, *Phyllophaga* spp. In oviposition, the female alights upon the dorsum of a feeding beetle, which causes the latter to take flight, whereupon she inserts the

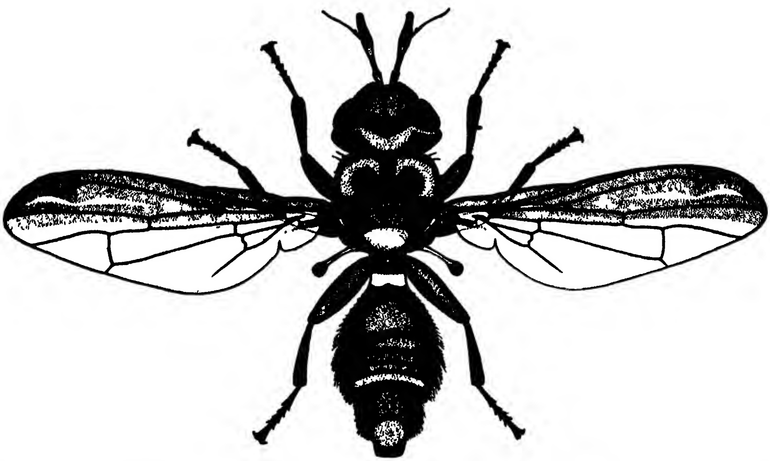


FIG. 186.—The adult female of *Adapsilia flaviseta* Ald. (*From Clausen et al.*, 1933.)

ovipositor through the thin exposed integument of the dorsum of the abdomen. Female beetles are more frequently attacked than the males. Death of the host takes place 10 to 14 days after parasite oviposition, and the puparium is formed within the dead host. There is a single generation each year, and the winter is passed in the pupal stage.

Adapsilia flaviseta Ald. is a common parasite of beetles of the genus *Popillia* in India (Clausen *et al.*, 1933). The adults are diurnal in habit, as are the hosts. The manner of oviposition is similar to that given for *Pyrgota undata*. In contrast to the habit of the latter species, its attack is principally upon male beetles, 88 per cent of the hosts being of this sex early in the season. This figure declines to 60 per cent during the latter portion of the period, when the ratio of male beetles becomes considerably reduced. The egg hatches 3 days after deposition, and the larval period covers 12 to 15 days. The host beetle is killed by the parasite larva shortly after its second molt, which is 12 to 14 days after the egg is deposited. A single generation is produced each year, and hibernation

takes place in the puparium within the bodies of the dead host beetles in the soil.

The unpublished reports of R. W. Burrell contain information on the habits of *Maenomenus ensifer* Bezzi as a parasite of adult beetles of *Anoplognathus olivieri* Dalm. in Australia. Its oviposition habit differs from those of the species already mentioned in that attack occurs while the host rests upon the foliage, the ovipositor being brought forward between the legs and inserted through the intersegmental membranes, or possibly through the anal opening. Ten to twenty individuals normally mature in each host, and a maximum of 33 was secured. Pupation

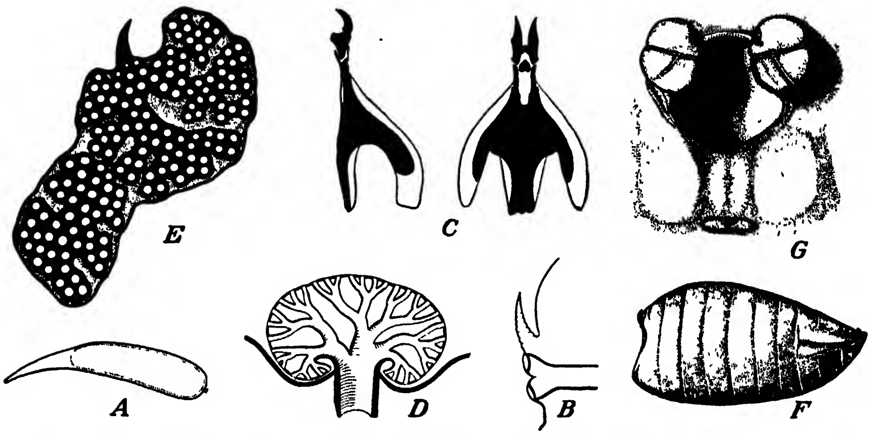


FIG. 187.—Details of the immature stages of *Adapsilia flaviseta* Ald. *A*, the egg; *B*, posterior spiracles of the second-instar larva; *C*, mouth hooks of the third-instar larva; *D*, sagittal section of the anterior spiracle of the third-instar larva; *E*, posterior spiracle of the third-instar larva; *F*, puparium; *G*, posterior view of the median depression of the puparium, showing the spiracles at the dorso-lateral margins. (*From Clausen et al.*, 1933.)

takes place externally between the elytra and the abdomen of the dead host in the soil.

On the basis of the information available regarding the habits of *Pyrgota* and *Adapsilia*, it may be concluded that these and other species of similar habit can be of very little value in the control of scarabaeid pests. The long larval period makes it quite probable that a portion of the oviposition potential of female hosts is realized before death. The pronounced preference of *Adapsilia* for male hosts greatly reduces its value, inasmuch as the portion of its effective reproductive capacity which is expended upon that sex is wasted. The death of male beetles contributes nothing to the reduction of the population of the following generation, even though it perpetuates the parasite.

IMMATURE STAGES OF *ADAPSILIA FLAVISETA* ALD.

The egg (Fig. 187*A*) measures 1.3 mm. in length and 0.25 mm. in width, with the posterior third drawn out to a narrow point. It is distinctly curved, and the smoothly

rounded anterior end bears a button-shaped micropyle. The first-instar larva is distinctly segmented, widest in the mid-abdominal region, with the caudal segments much narrowed, the mouth parts much reduced, and the single pair of spiracles of simple form. The second-instar larva is more robust and bears numerous papillae in a transverse band on each segment. The anterior spiracles are simple and very small, whereas the posterior pair (Fig. 187*B*) have two openings, one above the other, and are surmounted by a heavy, dorsally directed hook or spine. In the third-instar larva, the anterior spiracles (Fig. 187*D*) are stalked and fan-shaped, with many openings, whereas the posterior pair (Fig. 187*E*), situated at the dorsal rim of a large median depression, are very large and consist of three main lobes, with a dorsally directed hook or spine at the inner dorsal margin. They are markedly convex, with the ventral lobe curved beneath the rim of the depression. The puparium (Fig. 187*F*) is keel-shaped and brown to reddish-brown in color, with the anterior spiracles stalked. The median posterior cavity of the larva and puparium is common to a number of species, though Davis states that it is lacking in *P. valida* Harr.

AGROMYZIDAE

The larvae of this family are predominantly phytophagous in habit, many species being known to mine the leaves of plants, and among them are a number that are serious crop pests. Those of the anomalous genus *Cryptochaetum*, however, are all internal parasites of Homoptera. Thorpe (1931) lists the eight species that have been described, of which the host preferences of four are known. The hosts are all monophlebine Coccidae with the exception of several questionable records from *Dactylopius*. He has since had the opportunity of examining the larvae and puparia of the species occurring upon *Drosicha corpulenta* Kuw. in Japan, which has heretofore been recorded as *C. grandicorne* Rond., and states that it is distinct from any that have been described. This species, recorded upon *Drosicha* and *Icerya seychellarum* Westw., is a very effective parasite of the latter but does not attack *I. purchasi* Mask. (Kuwana, 1922). It is quite probable that two species are involved and that the form from *Icerya* may prove to be one of those recorded upon that genus in other parts of the world. In view of the parasitic habits of *Cryptochaetum* and the distinctive morphological characters of the larvae and pupae several authors believe that it should constitute a separate subfamily or family, and it has recently been set apart under the name Cryptochaetidae.

The Australian *C. iceryae* Will., which attacks *I. purchasi*, is the best known of the genus. It was established in California in 1888 as a result of Koebele's importations and has proved quite effective in certain sections. Its status as a controlling factor has been largely obscured by the more conspicuous *Rodolia cardinalis* Muls., which was introduced at the same time. *C. iceryae* has since been established in Chile and unsuccessfully colonized in several other countries.

An account of the biology and habits of *C. iceryae* has been presented by Smith and Compere (1916; recorded as *Lestophonus monophlebi*

Skuse) and later in more detail by Thorpe (1931). The adults are sluggish and feed largely upon honeydew. Freshly emerged female flies have well-developed eggs in the oviduct, and mating and oviposition take place within a very short time. Second-instar hosts are preferred, and at oviposition the fly stands upon the host and inserts the ovipositor by a downward thrust. The egg (Fig. 189*A*) is slightly kidney-shaped, measures 0.19 by 0.08 mm., and bears a minute funnel-shaped micropyle at the larger, anterior end. There is a considerable increase in size during incubation.

The first-instar larva is of the caudate type, though it is often referred to in this family as embryonic, for the body is a transparent cylindrical

FIG. 188.—The adult female of *Cryptochaetum iceryae* Will. (*From Smith and Compere*, 1916.)

sac 0.3 to 0.4 mm. in length and slightly curved, with very little indication of segmentation and with the caudal segment bifurcate and the lobes finger-like, with the tips broadly rounded. There is no trace of a tracheal system or of heart or sensory organs, and there are apparently no mouth opening or distinguishable mouth parts.

The second-instar larva (Fig. 190*C*) is somewhat cylindrical and has 10 distinct segments, and the tails are of markedly variable diameter, somewhat shorter than the body and terminating bluntly. A few short, pointed cuticular spines occur in a transverse row on the dorsum of the second abdominal segment, and similar spines completely encircle the following five segments, almost completely covering the sixth and seventh segments of the abdomen. A simple closed tracheal system is present, and the longitudinal trunks, with little evidence of branching, extend from the first thoracic to the posterior margin of the seventh abdominal segment. During the latter part of the stage, fine branches, usually

six in number, are developed in the expanded bases of the tails. There is very little growth in this stage, and no blood flow can be distinguished.

The body of the third-instar larva is very similar in form to that of the preceding instar, the most noticeable difference being in the tails, which are now 1.5 to 2.0 times as long as the body. The bases of the tails are greatly expanded, being as wide as the preceding body segments, and the fragile filaments beyond the bulbs are of uniform diameter. The hypodermis of the tail, in this and the preceding instars, consists of a single layer of cells with enormous nuclei. The lumen of the tail is filled with blood, though no circulation can be detected. The tracheal system is still closed, and there is a dense network of fine branches just beneath the epidermis, several of which extend into the tails for about two-thirds of their length. Two transverse commissures occur in the anterior part of the body and one in the last abdominal segment.

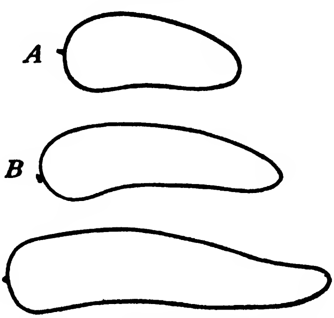


FIG. 189.—Eggs of *Cryptocheatum*. *A*, *C. iceryae* Will.; *B*, *C. grandicorne* Rond.; *C*, *Cryptocheatum* sp. from *Drosicha* sp. in Japan. Drawn to same scale. (*A and B, from Thorpe*, 1931, '34.)

The fourth-instar larva differs markedly in several respects from those preceding it. It is very robust in form, and each of the 10 distinct body segments bears a band of minute setae. The tails are exceedingly long, being three or four times the body length, and, except for the basal bulb, are very slender, kinked, and irregular. The tracheal system is now complete, with spiracles on the anterior margin of the first thoracic segment and on the dorsum of the seventh abdominal segment. The anterior spiracles are sharply pointed, dart-like structures, heavily sclerotized and set in pits, whereas the posterior pair are distinctly dorsal in position and are in the form of exceedingly heavy, dark-colored hooks directed caudad. The latter are apparently completely closed, and the anterior pair is not open until late in the stage.

The puparium (Fig. 190*F*) is at first pale yellow but eventually becomes quite black. The 10 segments are distinct, and the operculum, which is dorsal, extends to the posterior margin of the third segment. The anterior spiracles, fully extended, are terminal in position. The tails remain attached to the puparium and are shrunken and brittle. The prothoracic spiracles of the pupa are internal and do not protrude through the puparial wall.

The first-instar larva derives its food directly from the body fluids of the host, which are absorbed through the delicate integument. Feeding upon the fat body begins in the third stage, and gross feeding takes

place in the final stage. Prior to the third molt, the larva is virtually incapable of movement, whereas this takes place freely in the final stage. Just prior to pupation, when the body contents of the host have been largely consumed, the anterior spiracles are extruded to their full extent and forced through the skin of the host, usually at the lateral margin. The host skin then dries and closely envelops the puparium. In consequence of this, the skin is broken at the time the puparial operculum is raised, permitting the fly to escape.

One to six individuals attain maturity in each host. The life cycle covers a period of approximately one month, and five or six generations are produced each season in California.

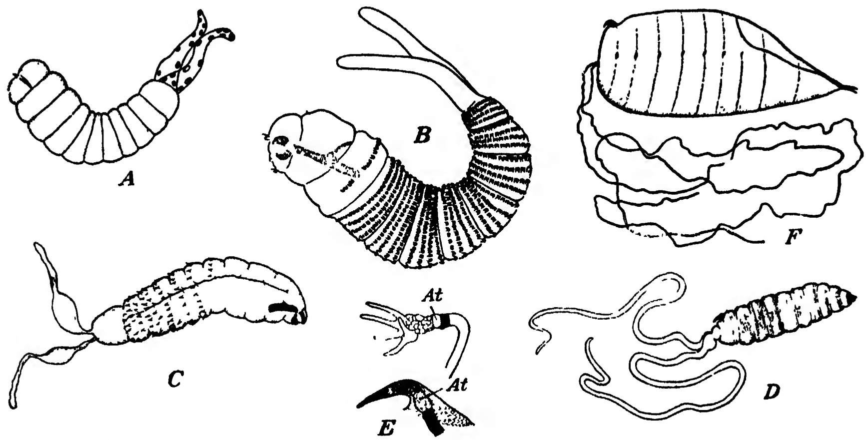


FIG. 190.—Immature stages of *Cryptochaetum*. *A* and *B*, first- and second-instar larvae of *C. grandicorne* Rond.; *C*, second-instar larva of *C. iceryae* Will.; *D*, third-instar larva of *C. grandicorne; E*, anterior (above) and posterior spiracles of same; *F*, puparium of *C. iceryae*. (*From Thorpe*, 1931, '34.)

The second species of the genus to be studied in detail is *C. grandicorne* Rond., which has been dealt with by Vayssiere (1926) and Thorpe (1934). This species is a solitary internal parasite of *Guerinia serratulae* F. in Europe. There are a number of marked differences in the morphology of the immature stages and in the manner of development, as compared with *C. iceryae*. There are only three larval instars rather than four. According to Vayssiere, the life history is well-adapted to the cycle of the host, and the pupal period of six months or more bridges the time in which the host is in the dormant phase of the first stage. Oviposition takes place only in the first-instar hosts after they have become fixed on the food plant.

The egg (Fig. 189*B*) is somewhat longer and more curved and the anterior end is relatively wider than in *C. iceryae*. The increase in size during incubation is much less. The first-instar "embryo" larva (Fig.

190*A*) is somewhat more elongate and is particularly distinguished by a pair of unpigmented mandibles projecting from the open mouth. The second-instar larva (Fig. 190*B*) has 11 body segments and bears a transverse row of digitate spines on the dorsum and sides of the third thoracic segment and four rows, completely encircling the body, on each of the following eight segments. The tubular tails increase greatly in length during the second stage. The tracheal system is similar to that of the third instar in *C. iceryae*. This instar may persist for three to four months. The third-instar larva (Fig. 190*D*) has the tail filaments shrunken and frequently broken off, so that in the latter part of the period they may be shorter than the body. The anterior spiracles are palmate in form and lightly pigmented, and those of the posterior pair show an opening near the base of the spine (Fig. 190*E*). Just prior to pupation, both pairs of spiracles are thrust through the skin of the host. Vayssiere states that the hook-like posterior spiracles of the third-instar larva are fixed in one of the large tracheae of the host, but the occurrence of this habit is not substantiated by Thorpe.

The biology and habits of *Cryptochaetum* sp. parasitic in *Drosicha corpulenta* and others of that genus in Japan present several points of difference from the two species already discussed (Clausen, unpublished notes). The adult flies feed principally upon the honeydew secreted by *Kermes miyasakii* Kuw., which occurs upon the same trees as the host insect. There are two generations each year. The summer brood of females oviposit in the young scales and pass the winter as young larvae within the living hosts. In this generation, both male and female scales are parasitized, and development is completed the following spring. These parasitized scales usually do not leave their hibernating quarters in crevices in the bark of the trunk of the tree. Male hosts are in the prepupal stage at the time of death, and emergence of the spring brood of *Cryptochaetum* coincides with that of the males of the host, this usually occurring May 10 to 25 in central Japan.

The spring brood of females oviposit in the *Drosicha* females, which at this time have just molted for the last time. The female parasite makes a deliberate examination of the host scale and, when satisfied as to its suitability, stands with the fore- and middle legs upon the lateral margin of the body and brings the ovipositor forward and inserts it just beneath the margin. The thorax appears to be the region preferred for oviposition.

The host individuals are of large size, and even those from which the overwintering brood emerges are large enough to provide sufficient food for several parasites. Only one develops to maturity in each host, and the puparia are always oriented with the anterior end toward the head of the host.

The egg of *Cryptochaetum* sp. (Fig. 189*C*) measures 0.35 by 0.08 mm. and is consequently considerably larger and more elongate than the eggs of either *C. iceryae* or *C. grandicorne*. The mature larva is 3.2 to 4.0 mm. in length, with the caudal filaments measuring 4.0 to 5.5 mm. The latter are of quite uniform thickness for their entire length, except for the basal portions, which are bulbous. The puparium is a deep red in color, and this shows through the integument of the host. The tails remain unbroken and turgid even after emergence of the adult fly from the puparium.

The life cycle given above, in which the parasite passes through two generations each year upon the same host generation, is markedly different from that given by Vayssiere and Thorpe for *C. grandicorne*, which has only a single generation annually and which provides for the long summer period when hosts are not available for oviposition by undergoing a prolonged pupal diapause.

The reproductive capacity of the females is known only for *C. iceryae* and *C. grandicorne*, both of which produce an estimated total of about 200 eggs. *C. grandicorne* and the *Cryptochaetum* sp. discussed above are solitary in habit, whereas one to six *C. iceryae* develop in each female of *Icerya purchasi*. In Australia, it is recorded that the remains of a single female *Monophlebus* showed 62 emergence holes of an undetermined *Cryptochaetum*, possibly *C. monophlebi* Skuse. The parasitized coccids were found beneath the bark of encalyptus trees and in the soil to a depth of 8 cm. Emergence of the adult parasites extended over a period of four months.

OCHTHIPHILIDAE

The entomophagous species of this family of small flies are found principally in the genus *Leucopis*, and the larvae are predaceous upon aphids, mealybugs, and scale insects, attack upon the last being limited to the nondiaspine forms. The great majority of species are restricted to aphid hosts. Several closely related but less common genera have the same food habits.

An undetermined species is recorded by Martelli (1908) as a common predator upon the eggs of *Filippia oleae* Costa in Italy. In ovipositing, the female fly stands either upon the egg sac or at one side of it, inserts the ovipositor beneath the margin or through the wax covering, and deposits an egg among those of the host. The entire contents of the sac are consumed by the one larva, and the cycle from egg to adult covers 30 days. There are four or five generations each year.

Several unnamed species are common predators upon aphids in Africa, and Cottam (1922) states that one is effective in controlling *Aphis sorghi* Theo. Cherian (1933) has studied the life history of *Leucopis* sp.,

as a predator of aphids in India, and describes the immature stages. The egg is 0.36 mm. in length, white, and ribbed longitudinally. The first-instar larva lacks the integumentary hairs, whereas the mature form has several fleshy processes on each body segment. The posterior spiracles of all instars are borne upon stalked processes, which are most pronounced upon the mature larva and the puparium. Before pupation, the larva exudes a considerable quantity of mucilaginous material which darkens quickly and firmly attaches the puparium to the substratum. The egg, larval, and pupal stages cover 2 to 4, 4 to 5, and 5 to 7 days, respectively.

Recently Maple (unpublished MS.) has made an extensive study of *L. bella* Lw. and *L. griseola* Fall.[1] in North America. The former is a

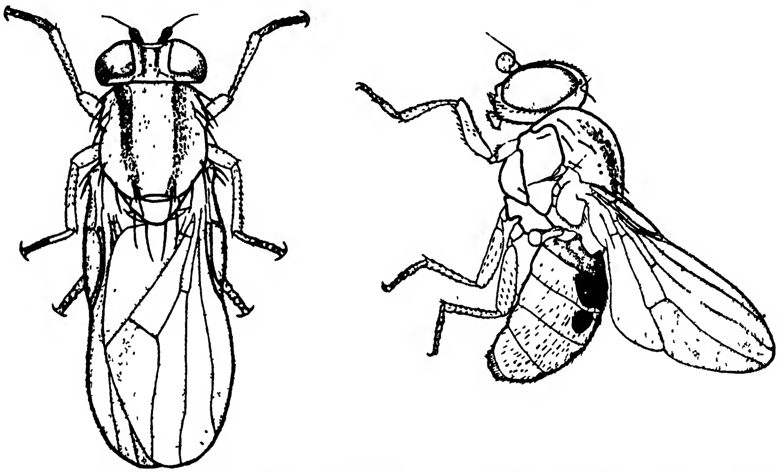


FIG. 191.—The adult female of *Leucopis bella* Lw., dorsal and lateral views. (*Drawings by J. D. Maple.*)

very common predator upon the eggs, and possibly the young larvae also, of dactylopine Coccidae, and the latter is an effective enemy of aphids. The eggs of both species measure approximately 0.5 by 0.16 mm. in size, with the anterior end somewhat pointed, and are pearly-white in color, with the surface bearing longitudinal ridges. They are deposited singly among the egg masses or colonies of the host and hatch in three to four days.

There are three larval instars in *L. bella*. The first is white in color, later becoming reddish, broadest in the abdominal region, and bluntly rounded posteriorly, and it tapers markedly toward the head. The integument is bare. The posterior spiracles are simple and borne upon prominent conical processes, and the anterior spiracles are minute. The

[1] This species has recently been studied also by Pruthi and Bhatia (1938). It is an important enemy of *A. gossypii* Glov. and other pests of that family in India.

third-instar larva (Fig. 192*A*) is 5.0 mm. in length and clothed only with minute setae. The posterior spiracles (Fig. 192*C*) are borne upon long and somewhat cylindrical processes, which are widely separated, diverging, and directed dorsad. Each spiracle consists of three curved, finger-like projections, each of which bears an opening at the apex. The larva of *L. griseola* is distinguished from that of *L. bella* by the possession of small, fleshy spines on all body segments.

In both species, the number of molts occasionally varies, apparently owing to temperature conditions. Some individuals have only two larval instars rather than the customary three.

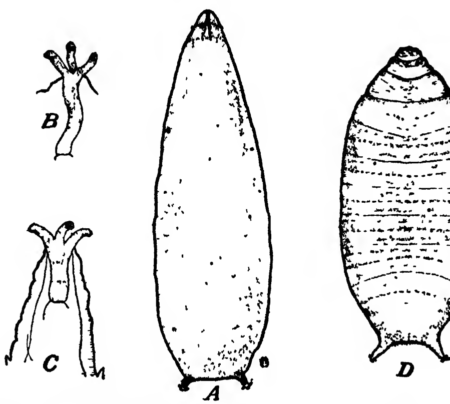


FIG. 192.—*A*, mature larva of *Leucopis bella* Lw; *B* and *C*, anterior and posterior spiracles of same; *D*, puparium. (*Drawings by J. D. Maple.*)

When pupation takes place among the egg masses of the host, an incomplete cocoon is spun, composed of a network of coarse threads. This possibly serves as a means of attachment. It is dispensed with in case pupation takes place in the open. The puparium (Fig. 192*D*) is dull reddish-brown in color and indistinctly segmented except for the anterior region. The stalked caudal spiracles of the mature larva persist unchanged, and there are no protruding prothoracic pupal cornicles.

Several generations are produced each year, and under summer conditions the egg, larval, and pupal stages are complete in 3 to 4, 8 to 12, and 13 to 14 days, respectively. In temperate regions, all species appear to pass the winter in the pupal stage.

Malloch (1921) has described the puparia of several predaceous species from Illinois. The puparium of *L. orbitalis* Malloch has minute, four-branched anterior spiracles, and the caudal pair are borne upon short, stout stalks lying closely adherent to the substratum upon which the puparium is formed. In *Leucopomyia pulvinariae* Malloch, the posterior spiracles are very small and sessile, differing in this respect from those described for other species of the family. All species are stated

to have the ventral side of the puparium more or less flattened, and in some the dorsum is depressed.

DROSOPHILIDAE

Although the great majority of species of this family develop in decaying fruits, fungi, and similar materials, yet a small number are predaceous or parasitic in habit. Larvae of the genera *Acletoxenus*, *Gitona*, and *Gitonides* are predaceous upon Homoptera, and *Titanochaeta ichneumon* Knab is recorded as having been reared from spider-egg sacs (Knab,

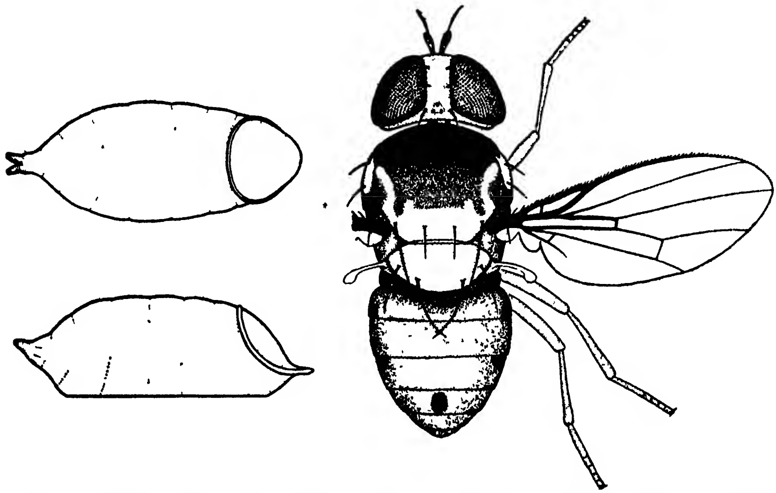


FIG. 193.—The adult female and the puparium, dorsal and lateral views, of *Acletoxenus indica* Ald. (*From Clausen and Berry*, 1933.)

1914). *Gitonides perspicax* Knab is known as a predator upon mealybugs in Hawaii and the Far East, and *Pseudiastata brasiliensis* C.L. attacks *Pseudococcus* in South America. *Rhinoleucophenga obesa* Lw. is predaceous in the egg sacs of *Aclerda campinensis* Hemp. in Brazil, and an undetermined species is found in those of *Orthesia* in the same country. *Acletoxenus* is apparently restricted in its host preferences to the Aleyrodidae, and a short account of the habits of *A. indica* Malloch (Fig. 193) has been presented by Clausen and Berry (1932). In some localities in Java, it is the dominant predator attacking *Aleurocanthus* spp. The eggs are somewhat oblong, measure 0.4 by 0.2 mm., and are covered with a white waxy incrustation. They are deposited singly on the leaf surface adjacent to mature host larvae or pupae. The larva is at first translucent white in color but later takes on a distinct greenish hue. It is very sluggish and never moves from the leaf on which the egg was laid. A single host cluster provides ample food to bring it to maturity. This larva in its later stages secretes an adhesive material over the body

which serves to attach various extraneous matter, including host exuviae, to it. Pupation takes place *in situ* upon the leaf surface, and the developing fly can be readily seen through the semitransparent puparial wall. The empty puparia are conspicuous among the host colonies because of their white color. The life cycle is complete in a period of about two weeks.

Several species of the dominant genus *Drosophila* are questionably of parasitic or predaceous habit. Bonnamour (1921) was able to rear *D. rubrostriata* Beck. from caterpillars of *Pieris brassicae* L. confined with gravid females. Death of the host larvae is probably induced by oviposition of the fly. Liquefaction of the body contents is rapid, and the larvae feed largely as scavengers. *D. paradoxa* Lamb and *D. inversa* Wlk. have been recorded as attacking the nymphs of the cercopid genus *Clastoptera* in tropical America. There is some question as to the role of the larvae attacking this host. Some authors consider that they are inquilines, feeding mainly if not entirely upon the spittle surrounding them. Lamb (1918), however, mentions that half the masses contained *D. paradoxa* larvae, which had their heads embedded in the bodies of the host nymphs. Baerg's (1920) observations on *D. inversa* revealed that the larvae normally lie diagonally across the dorsum of the host body, with the mandibles embedded in the fourth or fifth abdominal segment. He does not consider this species a true parasite and believes the larvae feed only upon the spittle. The fact that the larvae have a fixed position and embed the mandibles or even the entire head in the bodies of the hosts points to a closer relationship than would be necessary for a strictly scavengerous role. The larval habits and host relationships bring to mind those of the epipyropid larvae associated with Fulgoridae and related families.

MILICHIIDAE

The adults of this family are quite consistently insect feeders, and their feeding habits apparently represent a transitional stage between scavengerism and predatism. They are unable to kill their own prey but are dependent upon other predaceous species for their food.

Knab (1915) and De Peyerimhoff (1917) have given a summary of the known food habits of the family. A number of species of *Desmometopa* are definitely associated with asilid flies: they regularly attach themselves to the latter and maintain their hold until the prey is captured. Other species are more frequently associated with spiders, though they do not attach themselves to the body but feed upon the prey entangled in the webs, of which a majority were found to be bees. The above type of phoresy is an adaptation relating only to the feeding of the adults and consequently differs from that found in the Scelionidae and other

parasitic groups, where the object of the association is to reach the freshly laid egg mass for oviposition.

BRAULIDAE

The family comprises only the single genus *Braula*, with two species, both of which are associated with bees. The adults are degenerate in form as a result of their mode of life and lack wings and halteres. The head is large, with vestigial eyes, the scutellum absent, and the thorax not sharply differentiated from the abdomen.

The bee louse, *B. caeca* Nitz., is a commensal found upon honeybees and in their hives in various parts of the world. This species was long considered to be parasitic upon the adult bees themselves, but the investigations of Skaife (1921*c*) and Herrod-Hempsall (1931) have shown that the apterous adults feed only upon honey regurgitated by the bee. The worker bees and the queen are often very heavily infested, whereas very few of this species are found upon the drones. A maximum of 26 individuals was found upon a single queen. They usually attach themselves at the juncture of the thorax and abdomen or at the neck. For feeding purposes, they move to the head of the bee and, by taking up a position on the mandibles, either force or induce the bee to extrude the tongue, and they then feed upon the honey. They never feed upon the honey contained in the comb. Very little harm seems to result from this association.

The eggs are deposited at random over the brood comb or in the cells filled with honey. According to Skaife, the young crawl into the cells with the bee larvae and consume a portion of the food provided for them. The *Braula* larva forms a tunnel for itself from fragments of the cell wall, and pupation takes place within it. The cycle from egg to adult is completed in about three weeks.

CHLOROPIDAE (OSCINIDAE)

The family in general is phytophagous in habit and numbers among its members several important crop pests. A few species, however, are predaceous, such as *Siphonella palposa* Fall., which develops in the egg capsules of *Stauroderus* in Russia, and *Siphonella oscinina* Fall. in the egg sacs of spiders. *Pseudogaurax signata* Lw. (*Gaurax araneae* Coq.) is predaceous in the egg sacs of the black widow spider, *Latrodectus mactans* F. (Jenks, 1936). The spindle-shaped eggs are deposited upon the outer surface of the sac and hatch in two to three days, and the young larvae then burrow through the covering and feed upon the eggs. These are consumed in about two days, and pupation takes place *in situ*.

Chloropisca glabra Meig. is of particular interest because of its role as a predator upon the sugar-beet root aphid, *Pemphigus betae* Doane

(J. R. Parker, 1918). It is stated to be the most effective of the natural enemies attacking this pest, and hundreds of individuals are found upon a single infested plant. In oviposition, the female crawls down the base of the plant, inserts the ovipositor by a backward thrust into a soil crevice, and deposits the egg. The aphids, rather than the plant, provide the oviposition stimulus, for no eggs are found about uninfested plants. The eggs hatch in 3 to 5 days, and each larva consumes up to 50 mature aphids during the 9 to 12 days required for its development. The pupal period normally covers about nine months, though a few individuals emerge in two to three weeks and there is consequently a partial second generation. *Anatrichus erinaceus* Loew is reported to be predaceous upon the larger larvae of the rice borer, *Schoenobius incertellus* Wlk., in Formosa.

There are various gradations in habit among the strictly phytophagous scavengerous, and predaceous species. The larvae of *P. anchora* Lw. and others of that genus have been observed feeding upon the cast skins of *Hemerocampa*, whereas those of *Botanobia darlingtoniae* Jones feed upon the dead insects trapped in the pitcher plant. Species of several genera have been observed living, in an undetermined capacity, in the burrows of other insects.

SCATOPHAGIDAE (CORDYLURIDAE)

Very little is known regarding the predaceous and parasitic habits of members of this family, the adults of which are known as dung flies. The adults are largely predaceous upon small Diptera of the families Mycetophilidae, Bibionidae, Simuliidae, and Anthomyiidae. *Scatophaga stercoraria* L., and probably other species, also, suck out the body fluids of the prey through a puncture made in the neck. A few species are recorded as attacking Cicadellidae, and others are said to be parasitic in caterpillars. This latter habit, however, has not been definitely proved.

ANTHOMYIIDAE

The family is a very common one in all parts of the world and is represented by a large number of species. Superficially, many of the adults resemble the housefly in general appearance. The adult flies are mainly predaceous in habit and most frequently attack other flies, often of the same family.

Hobby (1934) reviews the food habits of the adults of the family and lists *Coenosia*, *Lispa*, *Trichophthicus*, *Pegomyia*, *Prosaepia*, *Hylemya*, *Helina*, and *Ophyra* as genera having representatives of entomophagous habit. The species of *Lispa* are predaceous upon various aquatic larvae. The habit of predaceous feeding by the adults of this family may be more general than is at present realized. In the above-mentioned

genera, the mouth parts show several morphological modifications that pertain to this manner of feeding.

In respect to their food habits, the larvae are exceedingly variable; some are plant feeders, others are scavengers upon decaying vegetable matter, and a number are parasitic or predaceous upon the immature stages, and occasionally the adults, also, of other insects. The most important of the entomophagous forms, from the point of view of the natural control of crop pests, are the species of *Hylemya* and *Paregle* which develop as predators in the egg capsules of locusts. *Acridomyia* is parasitic in the larger nymphs of *Locusta* in Russia. *Muscina pabulorum* Fall. is reported to be the most important natural enemy of *Lymantria monacha* L. and *Dendrolimus pini* L. in Europe. *M. stabulans* Fall. feeds extensively upon the caterpillars of the above species and upon larvae of the housefly. R. C. M. Thomson (1937) has given an account of the food habits of a number of species and states that certain species of *Myiospila*, *Mydaea*, and *Hebecnema* are dependent in part, at least, upon living food for the completion of their development and that this is provided by the larvae of other Diptera present in the dung that they inhabit.

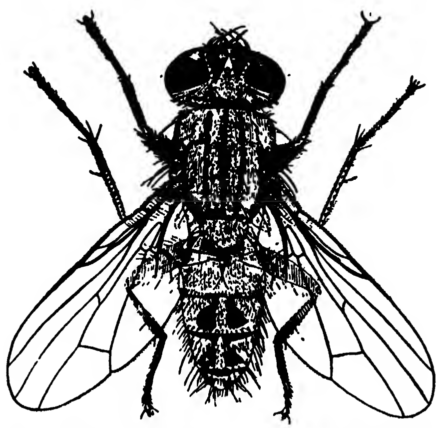


FIG. 194.—The adult male of *Lispa metatarsalis* Thoms. (*From Williams*, 1938.)

The larvae of the aquatic or semiaquatic species of the family feed consistently upon the larvae of other Diptera of suitable size that occur in the same environment. *Phaonia mirabilis* limits its attack largely to the larvae and pupae of mosquitoes, and *P. variegata* Meig., which is not aquatic, subsists solely upon mycetophilid larvae inhabiting fungi of the genus *Polyporus*. Several species of *Lispa* and *Lispocephala*, which are semiaquatic, feed upon *Chironomus* and other larvae (Williams, 1938).

Of the species that develop as predators in locust-egg capsules one of the most interesting and important is *Hylemya cilicrura* Rond., the well-known seed-corn maggot or shellat fly, which is a serious crop pest in many parts of the world. This range in food habits is exceptional, but it has been substantiated by observations in several countries. *H. cilicrura* has only occasionally been reared from locust eggs in North America, though Riley (1878*a*)[1] mentions that during one season it

[1] Listed in this and other references as *Anthomyia angustifrons* Meig. and *A. radicum* var. *caloptini* Riley.

destroyed about 10 per cent of the eggs of the Rocky Mountain locust. The most complete accounts of its habits have been given by Eberhardt (1930) and Blanchard (1933). The first-named author observed a maximum of 60 maggots in one egg capsule of the migratory locust in Dagestan, and in some localities nearly 100 per cent were attacked. Blanchard's account of its life history and habits as an enemy of *Schistocerca paranensis* F. in Argentina is quite complete. The female was noted to insert her ovipositor into the soil near the host egg capsule and to deposit a series of eggs at five-second intervals. A maximum of 80 is deposited by each female. Hatching takes place in a minimum of two days. The larvae immediately enter the capsule and begin feeding; if the food supply contained in one capsule is not adequate for their development, they may move to another. When feeding is completed, which is 8 to 12 days after hatching, they burrow a short distance away in the soil and pupate. In the summer months, the duration of the pupal stage is 8 to 15 days. Eberhardt states that pupation takes place 4 to 6 cm. beneath the egg capsules. There are three generations each year, and hibernation is principally in the pupal stage, though some adults and larvae may be found during the winter. The gestation period of the females is exceptionally long, covering 30 to 60 days, and adult life may extend to more than three months.

Acridomyia sacharovi Stack. is a gregarious internal parasite of the fifth-instar nymphs and adults of *Locusta migratoria* L. (Olsaufiev, 1929; Rukavishnikov, 1930). The female fly feeds upon the body fluids of the host, and the feeding puncture serves also as a point of insertion for the ovipositor. A maximum of 103 larvae have been found in a single host, though the average number that complete development is 20 to 30. Occasional hosts may recover from attack by this parasite if the number of larvae is small. The mature larva is readily distinguished by the spiracles, the anterior pair each having 11 papillae and the posterior pair nine openings, arranged in a three-quarters circle. The first brood of adults appears in the field in June, and there are at least three generations each year. The winter is passed in the pupal stage in the soil.

The greatest degree of adaptability to a predaceous life under special conditions is exhibited by *Phaonia mirabilis* Ringd., the larvae of which are aquatic in habit and feed upon the larvae and pupae of mosquitoes (Tate, 1935). The eggs (Fig. 195*A*), which are white, 1.8 mm. in length, ventrally keeled, and with lateral flanges, are deposited upon the surface of water contained in recesses in tree trunks, etc. The larvae that emerge from these eggs are remarkable in having all the characters of typical third-instar cyclorrhaphous larvae (Fig. 195*B*). This was verified by an examination of larvae still within the egg; consequently, the early appearance of this form is not due to rapid molting after

hatching. So far as could be determined, no molts take place during the active larval stage. There are three groups of long, slender hairs, supposedly sensory in function, on the ventral surface of the thoracic segments; and paired retractile protuberances (Fig. 195*E*), surmounted by numerous curved hooks, are present ventrally on the second to eighth abdominal segments. The anterior spiracles (Fig. 195*D*) are four- or five-lobed, and the posterior ones (Fig. 195*C*) have three openings. The tracheal system is appreciably modified for aquatic life, the main lateral

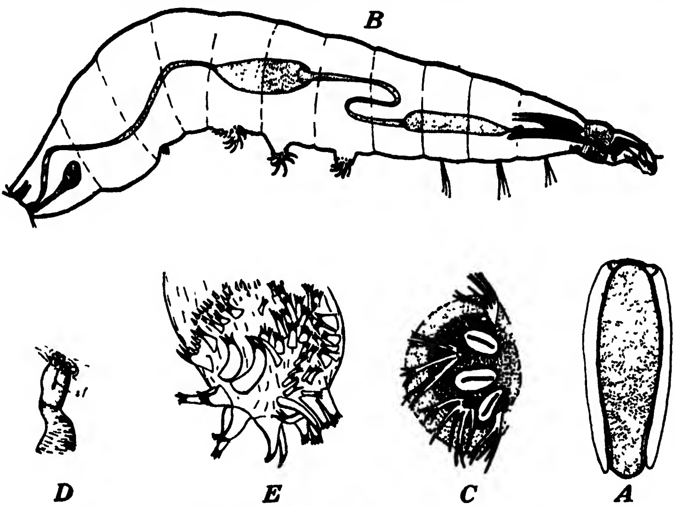


FIG. 195.—*A*, the egg of *Phaonia mirabilis* Ringd.; *B*, a one-day-old larva, with the caudal portion turned to give the dorsal view, showing thoracic and abdominal expansions of the tracheal trunk and a bladder-like structure arising at the juncture of the trunk and the posterior spiracle; *C*, a posterior spiracle of the same; *D*, an anterior spiracle; *E*, one of the ventral abdominal pseudopods. (*From Tate*, 1935.)

trunks being expanded into two large reservoirs, one lying in the thorax and the anterior portion of the abdomen, and the other in the mid-abdominal region; near each posterior spiracle, a short, stout trachea is given off which terminates in a blind sac. The mouth parts are well-developed.

The precocious assumption of the third-instar characteristics by the larva at the time of hatching is doubtless correlated with the predatory role that is immediately assumed, for the larva is under the necessity of overcoming an active host in water. It swims freely, either entirely submerged or with the posterior spiracles protruding through the surface film. When a mosquito larva or pupa is encountered, it is quickly encircled by the anterior portion of the body and firmly grasped with the ventral protuberances. The number of mosquitoes killed is considerably in excess of that consumed, and each individual may account for more than 100 during its lifetime.

The duration of the egg stage is at least three to four days, and larval development requires one month and the pupal stage about two weeks. Pupation takes place in crevices in decaying wood slightly above the surface of the water.

Further information on the peculiar biology of *Phaonia* is presented by Thomson (1937), whose studies deal with *P. variegata* Meig. in Scotland. The eggs are deposited upon the upper surface of the pileus of fungi of the genus *Polyporus*, and the larvae are predaceous upon those of Mycetophilidae inhabiting the fungus. Tate's observations on the hatching of the third-instar larva from the egg were corroborated, and it was established by examination of the egg after hatching that the scarcely recognizable exuviae of a preceding instar are present. Thomson expresses the belief that hatching of the third-instar larva from the egg, now known to occur only rarely, will be found to be far more widespread in the family than is anticipated. He suggests that the occurrence of three active larval instars will prove to be the exception, rather than the rule, in species of *Phaonia* and *Mydaea*.

The larva of *P. variegata* differs from that of *P. mirabilis* in lacking the conspicuous ventral pseudopods, surmounted with hooks, upon the abdomen, which are replaced by bands of spines ventrally at the anterior margins of the first eight abdominal segments. The usual anal plate is found on the venter of the last abdominal segment.

Keilin (1917) describes the larvae of several additional species of *Phaonia* found in decaying wood, forest litter, etc. That of *P. keilini* Coll., which is found in very moist decaying wood, is similar to that of *P. mirabilis*, whereas the larva of *P. cincta* Zett., which inhabits wounds and rotting areas in trees, has the same adaptive modifications as *P. variegata*. His studies, which deal particularly with larval morphology, include, also, a discussion of a number of carnivorous species of the genera *Melanochelia*, *Graphomyia*, and *Allognota*.

CALLIPHORIDAE

The family is known principally through the blowflies of the genera *Calliphora*, *Lucilia*, etc., which develop mainly in decaying flesh. There are, however, a number of species that in the adult stage are predaceous upon other insects. Bequeart (1922) has summarized the information available upon the food habits of the genus *Bengalia*. The adults of *B. obscuripennis* Bigot capture and feed upon winged termites; *B. jijuna* F. and *B. depressa* Wlk. have the habit of robbing ants carrying their larvae and pupae, and they feed upon these immature stages. Other species may rob the ants of insect prey that they are transporting to the nest.

Stomorhina lunata F. departs from the general habit of the family in being predaceous in the egg capsules of *Locustana pardalina* Wlk. Obser-

vations by Potgieter (1929) in South Africa showed that 50 to 90 per cent of the egg masses are destroyed by the maggots, and as many as 50 eggs of the predator were found in a single egg capsule. The flies are very active at the time of oviposition by the host, and, as soon as one of the latter withdraws its abdomen from the ground, the flies rush to the spot and deposit their eggs in the still-fluid covering of the egg mass. Oviposition also takes place in partly hatched-out egg capsules. The partly grown larvae have been noted to migrate from one capsule to another for completion of feeding. Usually, 2 to 3 puparia are found in an egg capsule, though at times the number may be as high as 12. The life cycle probably covers less than one month under summer conditions. In East Africa, 20 per cent of the egg masses of *Schistocerca gregaria* F. were found to be infested during an outbreak following a 10-year period of absence; in view of this, the species is presumed to have a native host, which is as yet undetermined.

Mention may be made of the several species that are known to be of parasitic habit, though none is known to have an insect host. The familiar cluster fly, *Pollenia rudis* F., is an internal parasite of *Allolophora* and other earthworms. Accounts of its habits with descriptions of the immature stages have been published by Keilin (1911*b*, '15) and Webb and Hutchinson (1916). The eggs are deposited singly in crevices in the soil and hatch in three days. The first-instar larva is very active and may enter the host body either through a natural orifice or through the body wall. The latter manner of entry has been verified by De Coursey (1932). The posterior end of the body remains embedded in the aperture, thus permitting direct respiration. The egg, larval, and pupal stages cover 3, 13 to 22, and 11 to 14 days, respectively. One to four individuals may develop in each host.

Fuller (1933) has given an account of the life history and habits of *Onesia accepta* Malloch, parasitic in *Microscolex* and other earthworms in Australia. Living larvae are deposited, rather than eggs, and females have been found to contain 500 or more eggs in various stages of development. The larvae are deposited in the soil, but the manner of their entry into the host has not been determined. In their early stages, they are found just beneath the skin, and parasitized earthworms may be readily recognized by constrictions of the skin along the path followed by the larva, this being consistently in spiral form about the body. The third-instar larva enters the body cavity, often killing the worm at this time, and completes its feeding as a scavenger. The duration of the different stages corresponds quite closely to that given for the stages in *Pollenia*.

Another species that develops as an internal parasite is *Melinda cognata* Meig., the host of which is a snail, *Helicella virgata* Da Costa.

Keilin (1919) records the finding of eggs of this species in the mantle cavity and concludes that oviposition probably takes place while the hosts are *in copula*. The young larva bores its way into the kidney and lies with its posterior end protruding into the mantle or the pulmonary cavity. Death of the host occurs when the parasite larva is in its early third stage, and pupation of the parasite takes place within the host shell. The life cycle is completed in about 15 days.

SARCOPHAGIDAE

There is an exceedingly wide range in the food sources of the larvae of the Sarcophagidae. Many species are limited to carrion, others to manure; some are true parasites of higher animals or infest wounds. The majority, however, are parasitic or predaceous upon other Arthropods. An unusual degree of plasticity is revealed in the habits of the members of this family, and many are apparently only in the transitional stages leading to obligate parasitism.

HOST PREFERENCES

General reviews of the host preferences of the family have been given by Aldrich (1915) and Greene (1925*a*). The entomophagous representatives of the family are found in the subfamilies Sarcophaginae and Melanophorinae.

On the basis of the information now available regarding host preferences, a considerable number of the entomophagous Sarcophaginae are parasitic in the nymphs and adults of locusts. Well-known genera having this habit are *Sarcophaga* and *Blaesoxipha*. *Oophagomyia* and *Wohlfahrtia* are predaceous in the egg capsules of the same host group, and an occasional species of *Blaesoxipha* is both parasitic upon the active stages and predaceous upon the eggs. *Mantidophaga* is an internal parasite of the late nymphs and adults of Mantidae.

The second host group that is very frequently attacked by members of the same subfamily consists of the bees and social wasps. The relationship in some instances is strictly parasitic, whereas in others it is commensal. *Myiapis* and *Senotainia* are internal parasites of worker honeybees, and *Sphixapate* develops within the larvae. *Metopia* and *Brachicoma* are externally parasitic or predaceous upon the brood of wild bees, the latter genus attacking principally the bumblebees. *Hilarella* and *Miltogramma* develop upon the various insects which are stored in the cells of hunting wasps or upon the material with which the cells of bees are provisioned.

Several genera have widely different host preferences from those above-mentioned. Lepidopterous larvae and pupae often yield sarcophagid flies, and it had been believed that these were parasitic. Patter-

son (1911) investigated a series of species of *Sarcophaga* associated with the gypsy moth and came to the conclusion that they were scavengerous only. Tests showed that the young larvae were unable to effect entry into healthy larvae or pupae, and if artificially introduced into the bodies of living individuals they invariably perished. Species of *Agria*, however, are known to be predaceous upon lepidopterous pupae. *Eleodiomyia* has been reared from adult beetles of the family Tenebrionidae; *Scarabaeophaga* from pupae and adults of *Cotinus nitida* L.; and *Sarcophaga* spp. from adult Pentatomidae, Blattidae, etc. Others recorded are

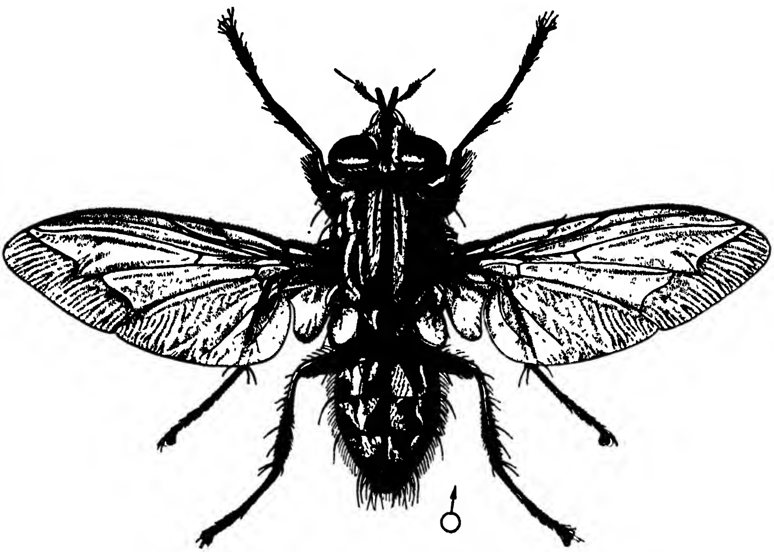


Fig. 196.—The adult male of *Sarcophaga kellyi* Ald. (*From Kelly*, 1914.)

Arachnidomyia from the egg sacs of spiders and various genera and species from snails.

A great range in host preferences is found among the parasitic and predaceous species of the genus *Sarcophaga*, as it is now constituted. Townsend and others have recently erected a number of new genera from species previously included in that complex, and those contained in the smaller groups show a considerable uniformity in host preferences and habits.

Relatively little is known regarding the insect hosts of the Melanophorinae, though species have been reared occasionally from spider-egg masses and from coleopterous larvae and adults. *Melanophora*, *Cirillia*, and closely related forms are parasitic in Isopoda (*Porcellio*, *Oniscus*, *Metaponorthus*), and some species of the subfamily have been reared from snails.

BIOLOGY AND HABITS

The Sarcophagidae are predominantly larviparous in their method of reproduction, and hatching of the eggs usually takes place in the uterus of the female shortly before deposition. Certain species of *Brachicoma* and *Agria* may deposit fully incubated eggs which hatch very quickly. *Parafeburia maculata* is an exception to the general reproductive habit of the family; it deposits membranous eggs which require a definite and relatively long period of external incubation. A number of related genera are believed by Thompson to have the same habit.

The gestation periods of the larviparous species are quite uniform and range from 10 to 16 days from the time of mating. The period of larviposition is relatively short and seldom exceeds 10 days. The reproductive capacity is not high; the production of a maximum of 285 larvae by *Blaesoxipha lineata* is the highest recorded for the family. Gravid females of *S. caridei* contain 100 to 200 eggs and larvae in the uterus, and *Wohlfahrtia euvittata* is said to produce a maximum of 131 larvae.

The greater part of the information regarding the habits and host relationships of the Sarcophagidae relates to the species that are parasitic in the nymphs and adults of locusts or are predaceous upon their eggs. The principal references to these species are: *B. filipjevi* Rohd. and *B. laticornis* Meig. (*grylloctona* Lw.) (Olsaufiev, 1929; Wood, 1933), *B. lineata* Fall. (Baranov, 1924; Olsaufiev, 1929; Rukavishnikov, 1930; Wood, 1933), *S. caridei* Brethes (Blanchard, 1933), *S. destructor* Malloch (Wood, 1933), *S. kellyi* Ald. (Kelly, 1914*a*), *Sarcophaga* spp. (Kunckel d'Herculais, 1894), and *W. euvittata* Vill. (Potgieter, 1929).

Although the majority of these species attack both nymphal and mature hosts, yet several, particularly *B. lineata* and *S. kellyi*, show a decided tendency to limit themselves to the adults. Wood states, however, that very few healthy locusts are attacked by the former species and that parasitic development is normal only in young adults. *S. destructor* is both parasitic and scavengerous in *Schistocerca* in the Sudan and shows a marked preference for mutilated hosts.

The method of attack and manner of larviposition differ appreciably among species. The females of *B. filipjevi* "squirt" their larvae with some force onto the end of the abdomen of the host while the latter is resting or feeding, whereas *B. lineata* places them on the upper side of the hind wings of the host while in flight. *B. laticornis*, on the other hand, inserts the ovipositor between the valves of the genital opening of the moving, though not flying, host. *Sarcophaga kellyi* strikes its host while in flight and places the maggot on the underside of the open hind wing, whereupon the locust falls to the ground. *S. caridei* deposits its larva on the venter of the flying or jumping host.

In *B. lineata*, *S. kellyi*, and *S. caridei*, the maggots effect entry into the body of the host through the thin membrane at the base of the wing, whereas *B. filipjevi* does so through the membranes of the abdomen or through the genital opening. The latter habit is similar to that of *Eleodiomyia* in attacking tenebrionid beetles. It has been pointed out by Wood that the maggots of *S. destructor* readily enter freshly molted hosts but are unable to do so in case the integument is fully hardened.

The death of the host usually takes place within a relatively short time after the larvae have entered the body. The mature larvae of *B. lineata* and *S. caridei* emerge from the host while the latter is still alive, and some parasitized individuals may recover; but the hosts of *Wohlfahrtia* are usually dead before the larvae complete feeding. The point of emergence is usually through the thin membranes of the neck, though some individuals of *S. kellyi* are said to emerge through the anal opening.

Experiments by Wood upon immature *B. lineata* showed that 78 per cent recovered from the attack but only 38 per cent of these were able to reproduce thereafter. In *S. destructor*, he found that relatively little growth takes place so long as the host remains alive. The young larvae of this species attack the wing muscles, and death results primarily through infection; after this, development of the parasite is rapid. Only 16 per cent of the hosts containing one parasite larva succumbed to the attack, whereas 92 per cent died when two or more were present in the body.

If the hosts are immature at the time of attack, they do not attain the adult stage. The feeding of the larvae is confined largely to the fat body. The number of individuals that develop in each host is variable, being normally only 2 in the case of *B. lineata*, whereas in *B. filipjevi* the maximum is 11 and in *S. caridei* it is 9.

The percentage of parasitization of locusts by the Sarcophagidae previously mentioned is often high; yet there is much difference of opinion as to their value in suppressing infestations. H. E. Smith (1915) states that swarms of *Dissosteira longipennis* Thom. in New Mexico were almost wiped out by *S. kellyi*. According to Kunckel d'Herculais, the parasitization of *Schistocerca* by sarcophagids in Algeria was 69 per cent in 1889 and 75 per cent in 1890. The flies were noted to follow the host swarms, harassing them continuously. In the case of *Wohlfahrtia euvittata* in South Africa, 50 to 90 per cent of the individuals of *Locustana* were found to be parasitized, and in some localities this attack was responsible for the discontinuation of poisoning programs.

Several of the species that have been discussed as internal parasites of the nymphs and adults of locusts are also predaceous in the egg masses of the same host species. This range in habit has been recorded for

Sarcophaga opifera Coq. in British Columbia, and it has been surmised by Treherne and Buckell that the larvae, after leaving the body of the adult host, continue their development upon the eggs in the soil. In South Africa, it has been observed by Potgieter that *W. euvittata* is fully as important in this role against *Locusta pardalina* Wlk. as when parasitic upon the active stages. Approximately 50 per cent of the egg masses in one section were destroyed by this fly. The maggots are deposited in groups in the openings of partly hatched-out egg pods or in the froth at the upper ends of those freshly deposited or exposed. Larvae in various stages of development have been found upon the surface of the ground, and these individuals were migrating to other egg pods for further feeding.

The species that are parasitic or predaceous upon the brood of bees and wasps are largely of the genera *Brachicoma, Metopia,* and *Hilarella.* Bougy (1935) has given an account of the attack of *H. stictica* Meig. upon *Ammophila hirsuta* Scop. in France. The host stores its nest with noctuid larvae. The female fly appears while the prey is being transported to the nest, but she does not attempt to larviposit upon it at this time. It is only after the caterpillar has been placed in the cell and the *Ammophila* egg deposited that she evades the watchful host, enters the burrow, and places her own minute larva alongside the egg of the rightful occupant. This egg is consumed within 24 hours, and the larva then enters the body of the caterpillar and completes its development. Each individual may therefore be termed a predator upon the egg of *Ammophila* and an internal parasite of noctuid caterpillars.

B. sarcophagina Tns. is recorded as an internal parasite of the mature larvae and young pupae of bumblebees in North America. The living young are deposited on or in the brood cells; then they enter the body and feed until larval maturity is attained. Pupation takes place in the nest material at the bottom of the comb. *B. davidsoni* Coq. is said to deposit eggs directly upon the larvae; after one is consumed, the parasite larva enters other cells and attacks their occupants, also. *Metopia leucocephala* Rossi has been recorded from the cells of *Philanthus.* The females enter the host burrow for a short distance and there deposit their larvae, which must then find their own way to the cells, at times a distance of several feet away.

Adult honeybees are reported to be heavily parasitized by *Senotainia tricuspis* Meig. in certain parts of Russia. The larvae feed mainly in the thoracic region. The same habit has been recorded by Seguy (1930) for *Myiapis angellozi* Seguy.

Agria mamillata Pand. is predaceous upon the pupae of *Hyponomenta* in Italy (Servadei, 1931). The flies appear in the field in early June

and deposit their partly incubated eggs upon the caterpillars when they are mature but before the cocoons are formed. The young larva enters the body of the pupa and rapidly consumes the contents; it then penetrates the adjoining cocoons in turn and continues its feeding. Fifty or more pupae may be destroyed by a single larva before it reaches maturity.

Hallock (1929) has reared *S. latisterna* Perk. from various lepidopterous pupae and believes that it is at times a true parasite, though the parasitic relationship is not yet obligatory.

Several species that are parasitic in isopods of the genera *Porcellio*, *Oniscus*, and *Metaponorthus* have been studied by Thompson (1920*a*, '34) and details of their life histories and habits made known. These differ in a number of ways from the general habits of the family. The adaptive characters of the first-instar larvae, as well as the habits of the immature stages, indicate a closer biological affinity with the Tachinidae than is shown by any other members of the family.

Parafeburia maculata Fall. is a solitary internal parasite of the first two genera named above. Its unincubated eggs are probably laid in the general vicinity of the hosts or where they are in the habit of congregating and hatch in about one week. These membranous eggs give rise to planidium-type larvae. This is the only instance known in the Muscoidea in which this larval form hatches from membranous eggs that are unincubated at the time of deposition. The young larvae enter the body of the host through the soft cuticle separating the ventral sclerites or at the bases of the appendages.

After entry into the host, the larva is found with its posterior end fixed in a perforation in the integument, and a respiratory funnel is formed. The second-instar larva has a very thin skin, and tests by the biological-indicator method revealed that an exchange of gases takes place through it; in fact, the greater part of the oxygen requirements of the larva may be secured in this way. Pupation takes place within the remains of the dead host.

There is a definite effect upon the reproductive system and the secondary sexual characters of the host as a result of parasitism by *Parafeburia*. The ovaries of the female are atrophied, owing to absorption of fat by the parasite, and such females never develop the brood pouch.

Less complete information regarding *Cirillia angustifrons* Rond. is also presented by Thompson. Its general habits are similar to those given above for *Parafeburia*. The outstanding feature in the host relationships of these two species is the formation of the integumentary respiratory funnel by the larvae. This habit is unknown elsewhere in the family, though common in the Tachinidae, and indicates a higher

development of the parasitic relationship than has been attained by other species.

Life Cycle.—The cycle of the parasitic Sarcophagidae, from larviposition to emergence of the adult, is relatively short, being completed in 16 to 30 days, of which the larvae feeding period covers only 5 to 10 days. In *Wohlfahrtia*, larval maturity is followed by a resting period of 6 to 12 days, and the pupal stage then requires 16 to 30 days. Several generations are usually produced each year, and five or six are recorded for *S. kellyi*. The hibernation habit is known for *B. lineata* and *S. kellyi*, in both of which it is the mature larva rather than the pupa that persists through the winter.

The cycle of *P. maculata* in *Oniscus* and *Porcellio* differs from the general habit of the family. There is only a single generation each year; the adults appear in midsummer, and the winter is passed as a second-instar larva within the living host.

IMMATURE STAGES

The eggs of the Sarcophagidae are all of the membranous type, with the chorion delicate, transparent, and bearing surface reticulations.

The first-instar larvae of the parasitic species of *Sarcophaga*, *Blaesoxipha*, and other Sarcophaginae have 11 body segments, each of which bears narrow bands of setae at both margins. Anterior spiracles are lacking, and the posterior pair each have two small, circular openings. The larvae of *Miltogramma punctatum* Meig. and several others have been described and figured in great detail by Thompson (1921) and are representative of the subfamily. They present no special adaptive characters and are of the general muscoid type. For a detailed study of the first-instar larvae of *Sarcophaga*, including some parasitic species, the reader is referred to the recent paper by Knipling (1936).

The larvae of *P. maculata*, *C. angustifrons*, and related species (Thompson, 1920, '34) differ markedly from those of the Sarcophaginae and are distinctly planidium-like, with the integument pigmented and armored. The first-named species is said to have 12 body segments rather than the usual 11. The cuticular armature is well-developed and consists of small, rounded protuberances bearing groups of short, heavy spines, one of which is usually larger than the others. In *Cirillia*, the armature consists of small, dark scales, whereas in *Trichogena rubricosa* Meig. the somewhat hemispherical processes that bear the sclerotized plates have also what is apparently a sensory organ, which is cylindrical and surmounted by a bristle, at the summit of each. The posterior spiracles of *Parafeburia* are markedly dorsal in position. The mouth hooks are similar to those of the Sarcophaginae, with two closely appressed lateral teeth rather than the single median one, whereas the latter form is found in *Trichogena* and *Cirillia*. There is a single articulation at the juncture of the anterior and intermediate regions. The antennae of *Cirillia*, instead of being conical, are long and spine-like and arise from a broad, collar-like base.

The second-instar larvae of the Melanophorinae are quite similar to those of the Sarcophaginae and have the integument delicate, unpigmented, and with few setae. They are most readily distinguished from the preceding instar by the spiracles. The anterior pair is now present; these are fan-shaped, usually with five to seven small rays, and each is surmounted by a small aperture. The posterior spiracles have two

vertical parallel slits, of which the inner one is the shorter. In *Parafeburia*, the anterior spiracles are rudimentary; the posterior spiracles of *Styloneuria* have only a single slit, and those of *Trichogena* have three.

The mature larvae of the parasitic species can usually be distinguished from those of scavengerous habit by the reduction in the cuticular processes; the spine bands are narrower or almost absent, and the fleshy segmental spines or processes are lacking. The median depression of the last abdominal segment, characteristic of the family, is usually of smaller size, with the rim more or less smoothly rounded rather than having

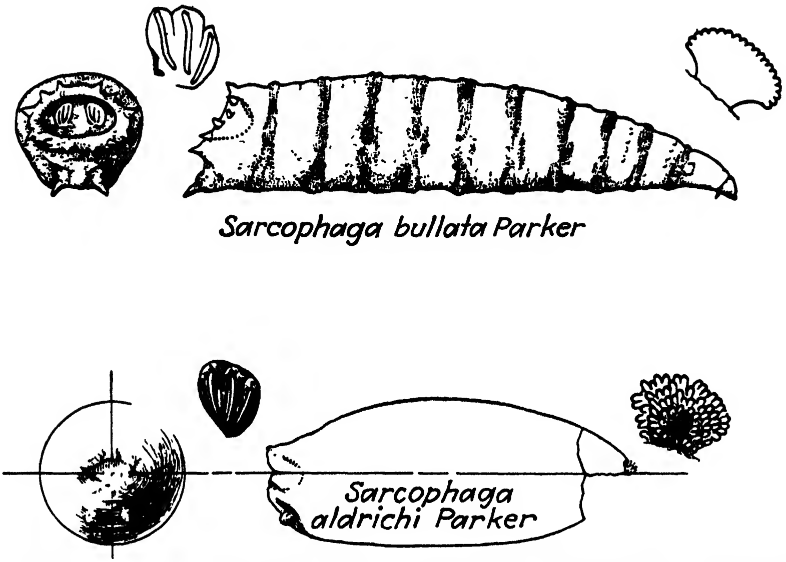


FIG. 197.—The mature larva and puparium, with details, of *Sarcophaga*. (*From Greene*, 1925.)

pronounced fleshy projections. The body tapers markedly cephalad, and the posterior abdominal segments are usually broadest.

The anterior spiracles of *Sarcophaga*, *Brachicoma*, and *Blaesoxipha* have 5 to 7 rays; there are 14 of these in *Agria mamillata*, and *Parafeburia* has 15 to 18 papillae scattered over the surface of the spiracle. According to Root (1923), who has studied the larval characters of a series of dung- and carrion-inhabiting species of *Sarcophaga*, the anterior spiracles of these forms have 10 to 35 rays. The posterior spiracles of all species are set in the median depression of the last abdominal segment, and each has three elongate or occasionally oval slits, which are almost vertical and parallel.

The buccopharyngeal armature has two articulations, and the paired mandibular sclerites are curved and usually sharply pointed, though in *Miltogramma punctatum* they terminate irregularly and bluntly.

The puparia are usually brown to reddish-brown in color, though that of *Melanophora roralis* L. is yellow, and the segmentation is indistinct. The posterior depression of *Blaesoxipha* is nearly closed by smooth, thick lips; this character serves to distinguish the genus from *Sarcophaga*. The last abdominal segment of *Trichogena* is much reduced, forming a tubercle surmounted by the spiracles. The prothoracic cornicles of the pupa do not protrude through the puparial wall. The internal pro-

thoracic spiracles are flattened, are somewhat circular in outline, and have the papillae arranged in double rows, radiating from the center as in *Miltogramma* and *Trichogena*, or in groups as in *Styloneuria*, *Cirillia*, and *Melanophora*. There are several hundred papillae in each spiracle of *Miltogramma;* in *Cirillia* and *Melanophora*, they are larger and number only 40 and 30, respectively.

TACHINIDAE

This is an exceedingly large family, of cosmopolitan distribution, and comprises flies of medium to large size and usually rather somber coloring. From the economic point of view, it is by far the most important of the dipterous families of entomophagous habit.

HOST PREFERENCES

For convenience in discussion, the host preferences of the family will be considered on the basis of the principal subfamilies. The Exoristinae are the dominant group, both in the number of genera and in the species that are known to be of importance as parasites of crop pests. The host preferences present an extensive range, with the majority of species parasitic in lepidopterous larvae and in adult beetles of the families Scarabaeidae, Chrysomelidae, and Carabidae. Familiar genera that parasitize caterpillars are *Compsilura*, *Anetia*, *Sturmia*, *Winthemia*, *Zenillia*, and *Exorista*. Upon adult beetles, *Eubiomyia*, *Centeter*, and *Chaetophleps* may be mentioned as representative. A relatively few genera and species parasitize the larvae of sawflies. A number of species attack the larvae of Curculionidae, Tenebrionidae, and Chrysomelidae, and occasional species are known to be parasitic in larvae of Tipulidae and Vespidae and in adult locusts, phasmids, and earwigs. Species of the genera *Meigenia*, *Doryphorophaga*, and *Paradexodes* attack chrysomelid larvae, and several species of *Siphona* are numbered among the relatively few parasitic enemies of tipulid larvae.

The Gymnosomatinae show an exceptional consistency in their host preferences; the majority are parasitic in the adults, and at times the nymphs, also, of the hemipterous families Pentatomidae, Pyrrhocoridae, and Coreidae. Well-known genera attacking members of these families are *Gymnosoma*, *Trichopoda*, and *Phasia*. A lesser number of species are parasites of locusts and adult beetles.

The Tachininae are predominantly parasites of lepidopterous larvae of stalk- and wood-boring habit or which are otherwise concealed. A number of genera, of which *Archytas*, *Bonnetia*, and *Eupeleteria* are well-known, are common enemies of cutworms and armyworms. An occasional species is recorded as parasitic in trypetid larvae. *Bigonicheta* departs from the general host preferences of the subfamily by attacking earwigs.

The Rutiliinae are a small group restricted to the Australian and South Pacific region; so far as known, they are limited in host preferences to the grubs of Scarabaeidae.

The Dexiinae contains a considerable number of genera that are parasitic in scarabaeid grubs, among which may be mentioned *Prosena, Dexia, Ptilodexia*, and *Microphthalma*. Adult Scarabaeidae are attacked by *Eutrixoides* and *Billaea*, and *Minella* has been reared from adult Chrysomelidae. Stem- and wood-boring lepidopterous and coleopterous

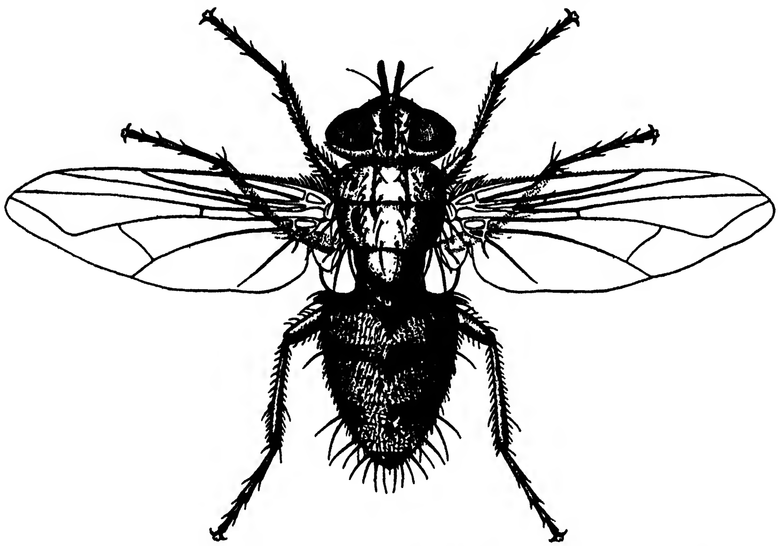


FIG. 198.—The adult female of *Trophops clauseni* Ald. (*From Clausen et al.*, 1933.)

larvae serve as hosts for *Theresia, Metagonistylum, Myiophasia*, etc. The genus *Thrixion* is parasitic in adult Phasmidae, *Ceracia* in locusts, and *Fortisia* in a chilopod of the genus *Lithobius*. The tropical American genus *Calodexia* is presumed to be parasitic in cockroaches, and it has been observed that enormous numbers of females are often associated with moving armies of ants (*Eciton* spp.), supposedly for the purpose of oviposition upon the host insects as they are driven from their hiding places.

The members of the Oestrinae that are parasitic upon insects attack largely the adults, though occasionally the grubs, also, of the Scarabaeidae. Among the genera having this habit are *Eutrixa, Eutrixopsis, Hamaxia*, and *Palpostoma*. *Rondanioestrus* is distinguished by its attack upon adult honeybees.

Attention has been called by Thompson (1938) to the relatively rare occurrence of dipterous parasites of Diptera, in contrast to the frequent attack by Hymenoptera upon their own order. Among the Tachinidae,

Siphona, *Admontia*, and *Trichoparia* have been reared from tipulid larvae, and several species of the first-named genus are common upon this host in certain sections. Other records of attack upon Diptera apparently must be considered as questionable. Considering their large size and exposed position, it is surprising that the larvae of Syrphidae are not subject to attack by members of this family.

The insect orders that have aquatic larvae are likewise virtually immune to attack by Tachinidae; yet the few Lepidoptera of such habit are readily parasitized, and the species responsible show pronounced adaptations for life in an aquatic environment. In many of these orders, the larvae are continually immersed in water, often at a considerable depth; yet certain of them leave it for pupation in the mud or sand near the water's edge. At this time, they would be vulnerable to attack, particularly by species having planidium-type larvae.

A considerable number of species of Tachinidae are apparently specific in their host preferences, but at the other extreme are species that have a much wider host range than is known in any other group of parasitic insects. The outstanding example of the latter class is *Compsilura concinnata* Meig., for which approximately 100 different hosts are recorded in the United States alone (Webber and Schaffner, 1926), these representing three orders and 18 families, and the known hosts in other countries will doubtless increase that number considerably. In general, it may be said that the species of this family are less restricted in their host range than are the Hymenoptera.

A great many species of native Tachinidae show a degree of parasitization and effectiveness comparable to that attained by introduced species. In northern Japan, *Centeter cinerea* Ald. destroys approximately 90 per cent of the adult *Popillia japonica* beetles, in alternate years, within 6 to 10 days after their emergence. These are the years of beetle abundance, whereas in the years of low population the parasitization is much less. The species is undoubtedly responsible for suppressing the pest to a noneconomic level in that country. In North America, the red-tailed tachina fly, given as *Winthemia quadripustulata* F.,[1] frequently destroys 50 per cent of the armyworm population, and at times the parasitization approaches 100 per cent. *Trichopoda pennipes* F. likewise builds up to a high level and at times destroys up to 80 per cent of the adult squash bugs and of several Pentatomidae. In Europe, *Ernestia rudis* Fall. is reported to parasitize a very high percentage of the pine

[1] There is considerable doubt as to the true identity of the species dealt with under this name. Reinhard states that the common red-tailed species attacking armyworms in North America is not *W. quadripustulata* and that several species are represented under that name in the biological studies which are reviewed in the following pages.

moth, *Panolis flammea* Schiff. The remarkable capacity for increase by the Tachinidae under field conditions is shown by *Paradexodes epilachnae* Ald., of which colonies of 100 to 200 were able to build up to a parasitization of 50 per cent or more in relatively heavy infestations of *Epilachna* over a radius of several miles from the point of release within two generations.

In net effect, the family may be considered as distinctly beneficial, for the great majority of species are primary parasites of plant pests. Unlike the major families of parasitic Hymenoptera, which have a varying portion of their species of hyperparasitic habit, there are none in this category in the Tachinidae.

Certain species are harmful because of their direct attack upon hosts that are themselves beneficial. From the point of view of monetary loss, the several species that attack silkworms in the Far East are unquestionably the most important of this group. Before adequate control measures were developed, the loss of silkworms from this cause in Japan was at times as high as 80 per cent. These parasites also serve as vectors of the pebrine disease. Other instances of parasitization upon beneficial insects are found in the species that attack adult Carabidae and honeybees. These, however, are not of general distribution and usually are not sufficiently abundant to affect the host population seriously.

A considerable number of species of the family have been successfully utilized in the biological control of crop pests. One of the outstanding examples is the control of the sugarcane beetle borer, *Rhabdocnemis obscura* Boisd., in Hawaii through the importation of *Ceromasia sphenophori* Vill. from New Guinea in 1910. Even more spectacular is the reduction brought about in the infestation of the coconut moth, *Levuana iridescens* B.B., in Fiji by *Ptychomyia remota* Ald., which was imported from Malaya in 1925. In the latter region, its normal hosts are species of *Artona*, a closely related genus that also attacks coconut.

Less conspicuous results have been secured in several other instances. A high degree of parasitization of the gypsy moth and a number of other lepidopterous pests has been attained in the United States by *Compsilura concinnata* Meig., imported from Europe from 1906 to 1911. Though complete control was not effected, yet the parasite is believed to have exerted an appreciable check upon the infestations. The establishment of *Chaetexorista javana* B. & B., of Japanese origin, in the northeastern United States has resulted in periodic control of the oriental moth, *Monema flavescens* Wlk., though complete and continuous control is apparently prevented by the inability of the parasite to withstand the occasional very low temperatures that occur in that section.

Several species of Tachinidae have been employed in the attempt to control the sugarcane moth borer, *Diatraea saccharalis* F., in tropical

and subtropical America. The Amazon fly, *Metagonistylum minense* Tns., originally found in the Amazon region of Brazil, has been colonized in British Guiana and many islands of the West Indies since 1933 and has brought about an appreciable reduction of infestation in some places, particularly British Guiana, where commercial control has been secured.

BIOLOGY AND HABITS

The more extensive publications upon the biology and habits of the family are those by Nielsen (1909, '12, '18), Pantel (1910, '12), and Baer (1920, '21). A large number of papers have been presented that give detailed accounts of particular species, and Townsend, in his recent "Manual of Myiology" (1934 to 1939), contributes a large amount of new information, particularly relating to the reproductive habits and the egg and first-instar larval forms.

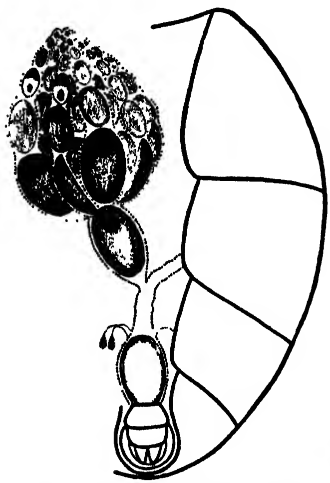


FIG. 199.—The female reproductive system of *Centeter cinerea* Ald. (*From Clausen et al.*, 1927.)

There is an exceptional uniformity in the general host relationships of the Tachinidae as compared with the parasitic Hymenoptera and other dipterous families. The larval stages are entirely internal during the feeding period, with the single exception of *Myiobia bezziana* Baran., which is stated by Beeson and Chatterjee (1935) to be an external parasite of the caterpillars of a wood-boring cossid in India. This, however, is such a radical departure from the otherwise consistent habit of the family that it requires a more thorough study.

The great majority of species of Tachinidae are solitary in habit; even among the gregarious species, it is only in exceptional instances that more than three or four develop in a single host, though sufficient food may apparently be available for a larger number. A maximum of 16 *Eubiomyia calosomae* Coq. is recorded from a single *Calosoma* beetle, whereas up to 28 *Palpostoma subsessilis* Malloch attain maturity in scarabaeid beetles in Australia. The highest number recorded is 110 *Achaetoneura samiae* Webber from a single *Samia* cocoon, and 550 *A. frenchii* Will. were reared from a lot of 44 *S. cecropia* L. cocoons. When superparasitization occurs, the surplus larvae are usually killed in the second or third stage, apparently through overcrowding or starvation, but at times by direct combat. If the number is excessive, all the larvae may die and the host continue to maturity, or the host, also, may die.

In one instance, a total of 147 dead larvae of *Achaetoneura* was found in a single *S. cecropia* larva.

The Female Reproductive System.—There are several modifications of the internal reproductive system of the female flies, dependent upon the type of eggs or larvae deposited. The basic type may be considered as that which produces the heavy-shelled macrotype egg and in which no appreciable uterine incubation takes place. *C. cinerea* (Fig. 199) is typical of this class. Each ovary comprises 9 or 10 ovarioles and has a

Fig. 200.—The female reproductive system of *Zenillia libatrix* Panz. At left, that of a freshly emerged female and, at right, of a mated and ovipositing female. (*From Dowden*, 1934.)

short oviduct leading to the uterus. The latter is likewise short and membranous for its entire length, with the stalks of the three spermathecae attached near the middle. In gravid females, each ovariole may contain one mature egg and a series of immature ones, and one mature egg is usually present in each oviduct and a single fertilized one in the posterior uterus. The daily production of eggs is relatively low but extends over a considerable period.

In the leaf-ovipositing forms producing microtype eggs, there are several adaptations. *Zenillia libatrix* Panz. (Fig. 200) (Dowden, 1934) may be taken as representative. Each ovary comprises 80 to 100 ovarioles, and in young females each of these contains about 14 eggs in various stages of development. The paired oviducts are long and slender, and the long posterior uterus is thick-walled for the greater portion of its length. The spermathecae are attached near the bases of the

paired oviducts. After fertilization, when the eggs descend into the uterus, this organ becomes very greatly enlarged and may contain several thousand eggs, which are packed irregularly within it. The coiled and expanded uterus may fill a large portion of the abdominal cavity. All species of this group have a large number of ovarioles, ranging up to 460 in the case of *Leschenaultia exul* Tns. (Bess, 1936).

A great many genera of the Exoristinae have this type of reproductive system and deposit microtype eggs. *Epidexia*, which has been placed

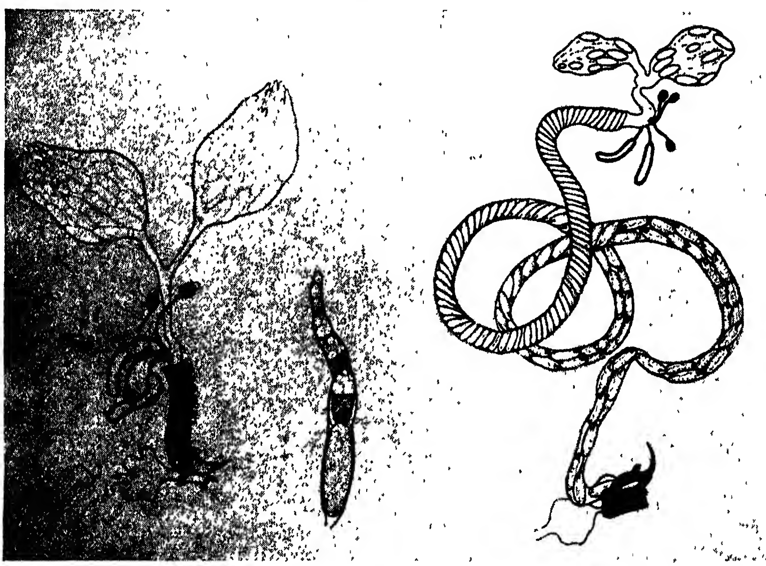


Fig. 201.—The female reproductive system of *Anetia nigripes* Fall. At left, that of an unmated female, with piercing organ removed and, at right, of a mated female six days after fertilization, showing piercing organ in position. (*From Dowden*, 1933.)

in the Dexiinae by Townsend, is the only member of that subfamily which is known to produce microtype eggs.

A third type is that represented by *Anetia nigripes* Fall. (Fig. 201) which injects its larvae into the body of the host. Each ovary consists of 12 to 14 ovarioles, and in unmated females the anterior and posterior uteri are of approximately equal length, with the spermathecae attached near the juncture. After mating, the eggs descend past the spermathecal openings into the posterior uterus, which becomes very greatly elongated and lies in four coils. The eggs most recently passed into the uterus lie transversely in an even row. But as they progress downward, they lie longitudinally and usually paired, with the head end directed cephalad with respect to the body of the parent female, and, as a consequence, the larva is ejected caudal end first. In the gravid females of some of the larger species, this "strap-like" uterus is very long, reaching its greatest

development in *Latreillimyia bifasciata* F. in which it measures 110 mm. in length (Townsend, 1936). The eggs range from fully incubated at the posterior end of the uterus to undeveloped at the anterior end. This form of reproductive system provides for the deposition of a relatively small number of larvae daily, though larviposition extends over a considerable period. In *Compsilura concinnata* and *Ernestia ampelus* Wlk., however, all the eggs in the uterus are in the same stage of development, permitting the deposition of the full quota of larvae in two or three days (Tothill, 1922). Culver (1919) points out that the maggots of this species lie in the reversed position in the uterus and are consequently ejected head first.

The final form is that of many of the species which deposit their maggots on foliage or on the surface of the soil. The uterus is more or less coiled and strap-like before fertilization; but after this is accomplished, it becomes much distended and filled with enormous numbers of eggs in all stages of development, these often lying in precise transverse rows in the anterior portion and longitudinally in the posterior section (Fig. 202). Townsend mentions that those of *Echinomyodes* are arranged with the utmost precision, in as many as 24 rows. This type of reproductive system provides for the deposition of a very large number of larvae in a short period of time.

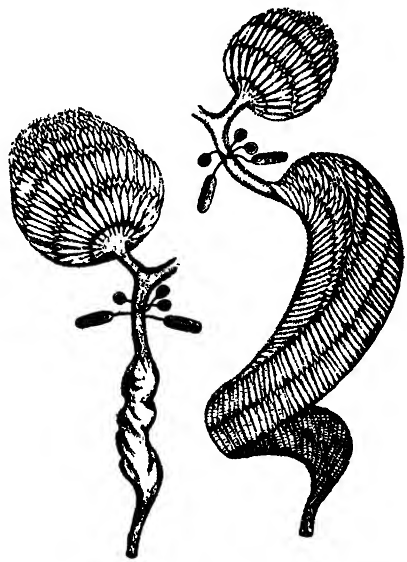


FIG. 202.—The female reproductive system of *Prosena sibirita* F. At left, that of an unmated female and, at right, after fertilization and incubation of the eggs. (*From Clausen et al.*, 1927.)

Among the species depositing larvae or fully incubated eggs, the posterior uterus serves as an incubation chamber; owing to the oxygen requirements during embryonic development, the walls of the uterus are abundantly supplied with tracheae.

Landis (1940) has made some interesting observations upon the rhythmic development of the eggs in the reproductive system of *P. epilachnae*. The total number of ovarioles ranges from 16 to 54, and each contains six eggs in various stages of development, these representing the full reproduction capacity of the female. Each egg has a "brood" relative in the entire series of ovarioles, and together they descend into the oviduct at approximately the same time. The successive "broods" descend in turn, and they may be distinguished in the uterus by the stage

of incubation attained, the first batch being fully incubated and each following one showing less development than the one preceding it.

The females of the species that inject their eggs or larvae into the body of the host require an extensive modification of the external reproductive apparatus. The form that this takes is dependent upon the kind of host attacked and the amount of force required to effect penetration. The more simple adaptation is that of the species that attack caterpillars, in which only a relatively thin and flexible integument is pierced. Adaptation for penetration of such hosts is found in a number of common genera, such as *Anetia*, *Compsilura*, *Lydella*, etc. The sixth abdominal segment is developed into a curved, sharply-pointed, thorn-like process. This structure, termed the piercing organ, is deflected downward and in some species lies along the mid-ventral line when not in use. It is grooved along the outer convex side, and the ovipositor glides along this groove in the deposition of the eggs or larvae. There are thus two distinct acts involved in larviposition: first, the puncturing of the host integument, and then the insertion of the ovipositor in the wound for deposition of the egg or larva. In the species that deposit larvae in this way, they are usually placed directly between the peritrophic membrane and the cellular wall of the mid-intestine rather than free in the body cavity of the host, and are then left to their own devices to reach their ultimate destination.

The most striking adaptation for deposition of the egg or larva internally is revealed in *Chaetophleps setosa* Coq. (Fig. 203*B*), a parasite of chrysomelid beetles of the genus *Diabrotica*, which has been described and figured by Walton (1914) under the name of *Neocelatoria ferox* Walt. and has since been studied in detail by Bussart (1937). Not only is the sixth abdominal segment modified into a very long piercing organ, more than half the length of the abdomen, but the second abdominal segment is greatly produced ventrally into a laterally compressed structure which bears at its tip a considerable number of heavy, flattened, spine-like processes directed somewhat caudad. In larviposition, the fly pounces upon the beetle; the latter turns upon its back, whereupon its abdominal region is grasped in pincer-like fashion between the piercing organ and the extension of the second segment. The ovipositor is then driven through the elytra and into the dorsum of the abdomen. Houser and Balduf (1925) state, however, that many beetles are attacked while in flight or after alighting but while the wings are still spread and the ovipositor is inserted through the thin dorsal integument of the abdomen. Bussart states that oviposition is accomplished only while the beetles are in flight. The above modification of the abdominal structure of the female is clearly an adaptation for holding a hard-bodied host during insertion of the ovipositor. *Celatoria diabroticae* Shim., which also

attacks *Diabrotica* beetles, is similarly modified (Fig. 203*A*). A similar adaptation, evidently for the same purpose, is found in the Conopidae, which are parasitic in adult bumblebees and various of the larger wasps.

Habits of the Adult.—Among the great majority of species, the emergence of the adults takes place during the early morning hours, though it has been noted that those of certain species of crepuscular or nocturnal habit do so during the late afternoon and early evening. They feed upon honeydew secreted by aphids, scale insects, and leaf hoppers and upon various plant secretions, particularly of the nectar glands. Some species of Dexiinae, such as *Prosena sibirita* F., are equipped with an exceptionally long proboscis, by means of which they are able to feed at blossoms, mainly of the Umbelliferae. In laboratory rearing, it was

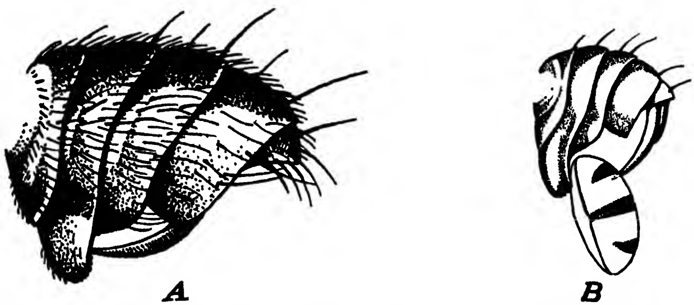


FIG. 203.—*A*, Lateral view of the abdomen of the female of *Celatoria diabroticae* Shim., showing the piercing organ; *B*, the same view of *Chaetophleps setosa* Coq., showing the probable manner of oviposition in host beetles. (*From Walton*, 1914.)

found by Landis that females of *Paradexodes* confined in cages and fed with sugar and raisins live longer if the cage is dirty rather than clean. From this it is inferred that the yeasts and other materials obtained from waste matter have a beneficial effect upon the flies.

Feeding upon the body fluids of the host occurs rather infrequently in the Tachinidae and is possible only in those species which have the piercing type of ovipositor. Bruneteau (1937) has noted that habit in *Doryphorophaga doryphorae* Riley, a parasite of the larvae of the Colorado potato beetle, and it is recorded also for *Anetia nigripes*.

It has been mentioned that the adults of some species are crepuscular or even nocturnal in habit, and this is most frequently correlated with a similar habit in the host stages that are attacked. It is not an invariable rule, however, as may be seen in *Hamaxia incongrua* Wlk. This species is active in the late afternoon and early evening hours, though one of its principal hosts, *Popillia japonica* Newm., is strictly diurnal and feeds during the morning and early afternoon, following which it enters the soil or seeks some place of concealment. Certain other scarabaeid hosts, particularly of the Sericinae, are strictly night feeders; yet there

is no appreciable difference in the extent of parasitization because of this apparently more favorable habit. The Australian *Palpostoma subsessilis* is likewise crepuscular, and *Cryptomeigenia theutis* Wlk. is nocturnal, as are the adult *Phyllophaga* which it attacks.

Mating normally takes place very soon after emergence from the puparium and in most species is accomplished during the morning hours in periods of bright sunshine, though *Carcelia gnava* Meig. and a few other species do so at dusk. Under laboratory conditions, mating is often secured most readily by caging one- or two-day old males with freshly emerged females. Temperature, light, and humidity are important factors influencing mating activities, and the optimum range is often quite narrow. Various means have been employed to stimulate activity, such as exposure in vials to bright sunlight, vigorous shaking of the cages, lining the walls of the cage with green cloth, etc. In his studies on *Metagonistylum*, Cleare (1939) has determined that light intensity is the most important factor and that mating takes place only within a comparatively narrow range.

The males are capable of fertilizing a considerable number of females, as is shown by records for *A. nigripes* (Dowden, 1933), of which 1 male successfully fertilized at least 13 females in a period of about four weeks, though later matings revealed a progressive reduction in the proportion of the eggs that were found to be fertilized. Repeated mating of the females has been noted in several species.

There is a considerable range in the duration of the period of gestation. The minimum is the two days recorded for *Ptychomyia remota*, though *Winthemia* requires only slightly longer. These species deposit unincubated eggs, and it is to be expected that the gestation period will be short. The shortest period recorded for those which deposit fully incubated eggs or maggots is that of *Palpostoma subsessilis;* this species was found by Burrell to contain fully developed larvae within four to six days after emergence from the puparium. In general, the larviparous species have a gestation period of 8 to 14 days, though this extends to as much as four weeks in the case of *Ernestia ampelus*. In this species, all maggots in the uterus are in the same stage of development, and deposition may be completed in two days or may extend over a period of one month (Tothill, 1922).

In his studies upon the females of a large series of parasitic Tachinidae, Townsend (1908) distinguished five modifications of the reproductive habit as follows: (1) host oviposition, (2) leaf oviposition, (3) supracutaneous host larviposition, (4) subcutaneous host larviposition, and (5) leaf oviposition. These are based upon the position of placement of the eggs or larva with respect to the host, and no distinct additions have since been made to this list. This author's conclusions were based

to a considerable extent upon the information derived from the dissection of gravid females, and he points out that not only can the type of egg be determined by such dissections, but useful clues as to the oviposition habit may thus be secured. Pantel (1910) has presented a somewhat different classification, distinguishing 10 groups and using as a basis the reproductive system of the female, the type of egg, the stage of incubation of the egg and the placement of the egg or larva at deposition (see page 345). In his recent "Manual of Myiology," Townsend (1934) lists 39 groups, the majority of which represent Tachinidae, on the same basis that is employed by Pantel, but utilizing also the general characters of the first-instar larvae. A useful distinction is made by this author between oviposition and larviposition. Oviposition is considered to refer to the deposition of all eggs adapted for attachment to surfaces, whether of flattened form or provided with a pedicel, and of which the embryo may be in any stage of development. Thus, the deposition of all microtype eggs, all macrotype eggs as herein defined, and unincubated membranous eggs come under this head. Larviposition, on the other hand, refers to the deposition of fully formed maggots, followed by their immediate activity, irrespective of whether they are naked or enveloped in the membranous chorion.

Reproduction in the family may be oviparous, ovoviparous, or larviparous, and various adaptive modifications have arisen as a consequence of these differences in habit. There are four general types of egg, the microtype, macrotype, pedicellate, and membranous. These are associated with certain morphological modifications of the parent female, which have already been mentioned, and serve, in one way or another, to aid the parasite to reach its goal, which is the body cavity or some internal organ of the host.

The females of species that deposit incubated eggs or larvae directly upon their hosts and consequently require the stimulus of the presence of the latter for normal oviposition or larviposition will, under stress of necessity, deposit them at random in order to reduce the internal pressure resulting from the constantly increasing number of eggs in the uterus. Those which inject them into the host body, however, will retain them indefinitely if hosts are not available, and they may finally die as a result of penetration of the body cavity by the imprisoned larvae, as has been observed by Tothill in the case of *Ernestia ampelus*.

Reproductive Capacity.—The reproductive capacity of the Tachinidae varies greatly among different groups and species and is related directly to the position in which the eggs or larvae are deposited with respect to the host and the hazards to which each species is subjected before the larvae reach the body cavity of the host. The minimum deposition of eggs or larvae occurs in those species in which the female injects the eggs

or larvae into the host body or deposits them directly upon the body. In this group, we find many of the most common and important species, such as *Compsilura concinnata, Trichopoda pennipes,* and *Winthemia quadripustulata.* The capacity of these species is approximately 100 to 200, with several apparently depositing less than 100. *Phorocera agilis* R.D. (Prell, 1915; Burgess and Crossman, 1929) has a capacity of over 200 eggs, deposited at the rate of 4 or 5 per day.

The next group comprises the species that deposit larvae or fully incubated eggs in the immediate vicinity of the host. *Bigonicheta setipennis* Fall. places its eggs very near to the host, or occasionally upon it, and its total is relatively low, being about 250, whereas others in which the association is not so close produce a higher number. Those which place them upon foliage and of which the hosts are free-living caterpillars deposit 400 to 1,000 eggs or larvae. Where the host is enclosed in a tunnel in a plant stem, as in the various cane borers, and the larva is deposited near the entrance hole, the number is usually in the neighborhood of 1,000. Gravid females of *Theresia claripalpis* v.d.W. contain more than 500 eggs and larvae (Jaynes, 1933), and Myers (1934*b*) mentions that *Metagonistylum minense,* likewise parasitic upon *Diatraea* and having the same general habits as *Theresia,* produces 500 to 700 maggots.

Among the parasites of white grubs, which deposit their eggs or larvae on the surface of the soil, *Prosena sibirita* often contains upward of 800 larvae and eggs in various stages of development, and Townsend mentions that approximately 2,000 eggs were found in the uterus of a female of *Microphthalma disjuncta.*

The final group comprises the species which deposit microtype eggs and those in which the larva is attached to the substratum by a membranous cup, consisting of the old eggshell, enveloping the caudal segments. The microtype eggs must be eaten by the hosts, whereas the fixed larvae are dependent upon passage of the host larva within reach. The chances of reaching the host are thus more or less equal, as is shown by the reproductive capacity of the two forms. In 1738, Reamur estimated that a female of *Echinomyia* contained 20,000 maggots, but this figure has been considered too high by later investigators of this species. Von Siebold estimated 7,000 in the case of *E. fera* L. Townsend, however, mentions 13,000 for *Echinomyodes,* which is by far the highest number determined by actual count. The uterus of a female of *Eupeleteria magnicornis* Zett. was found by the same author to contain approximately 3,200 eggs and maggots, and this was believed not to represent the full reproductive capacity. The records for species having microtype eggs range from 2,000 to 6,000.

The above unusual method of reproduction, in which the minute eggs are deposited apart from the host larvae and must be eaten by the latter

before hatching can take place, is now known to occur in a large number of species, principally of the subfamily Exoristinae. In 1908, Townsend recorded 14 species having this habit, and in 1910 Pantel listed European species of 8 genera. Since that time, a very large number in many genera have been found to reproduce in the same manner. The better known genera having this habit are *Exorista, Frontina, Gonia, Masicera, Sturmia, Gaedia, Chaetogaedia, Leschenaultia, Pales, Parachaeta, Prosopaea,* etc. This striking oviposition habit was first observed in *S. cilipes* Macq. (*sericariae* Rond.) by U. Sasaki in 1873, and the first record is that by H. Pryer in his catalogue of the Lepidoptera of Japan, published in 1884, in which he states, "I have noticed that the Uji, a diptera, which is parasitical upon it and causes an immense amount of damage, deposits its eggs about the larva on the leaves and not on the insect."

An extended account of the habits of the species was published by Dr. C. Sasaki, son of the discoverer, in 1886. A habit such as this was so far from the known habits of the family at that time that little credence was given to it for many years, and it was not until 1908, when Swezey's account of the habits of *Chaetogaedia monticola* Big. was presented and also that of Townsend upon several other species in the same year, that full credit was accorded to Sasaki's outstanding contribution to the knowledge of the habits of the family. The remarkable parallelism between the course of events here outlined for Tachinidae of this type, and that which takes place in the Trigonalidae of the Hymenoptera, is of special interest. In both cases, the eggs are minute, hard-shelled, deposited upon the food plant of the host, and capable of remaining viable for a long period; they are eaten by the host and finally hatch in the digestive tract, from which point the larvae migrate into the general body cavity or to a particular organ.

Stage of Host Attacked.—The great majority of species attack the host while it is in the larval stage. This habit is consistent among those which parasitize Lepidoptera, and none is known to attack the pupa directly, though some complete their feeding in that stage. A number of species, such as *Zenillia libatrix*, delay development beyond the first instar until host pupation has taken place. Those which deposit macrotype eggs upon the host body usually limit themselves to the late larval stages, whereas others may gain entry at almost any time during the larval period. *Prosena* and *Dexia* are able successfully to parasitize their scarabaeid grub hosts in any stage, though they do not complete feeding until the latter are mature. Tachinid parasites of chrysomelid larva, such as *Paradexodes*, at times successfully attack the prepupae and pupae, also.

An exceptional instance of emergence of a tachinid maggot from an adult moth has been noted by Edelsten (1933). A female *Zygaena lonicerae* Esp. emerged normally and lived for only two days, during which

she deposited 30 eggs. Ten days later a mature maggot of *Phryxe vulgaris* Fall. emerged from the body, after having completely consumed the contents. Previously, the emergence of a larva of this species from a living female of *Nyssia lapponaria* Boisd. had been reported. The emergence of moths of *Manduca atropos* L. from pupae that had yielded tachinid maggots, the latter having emerged from the wing pads, has been observed in several instances.

There are a large number of species of the family that attack only the adult stage of their hosts. This is true of practically all those which parasitize Hemiptera and Orthoptera. It is particularly noteworthy that many species which attack adults tend to limit their oviposition largely to the female sex. From the point of view of field control, this is a factor of considerable importance, for it results in maximum reduction in the host population over a period of time. *Centeter cinerea* deposits 80 to 95 per cent of its eggs upon the female beetles of *Popillia japonica* Newm., and other conspicuous examples of this habit are *Hyalomya aldrichi* Tns., which attacks mainly the adult females of the false chinch bug, *Nysius ericae* Schill., and *Thrixion halidayanum* Rond., which restricts itself to female Phasmidae. In contrast to this, the greater portion of the chrysomelid hosts of *Chaetophleps setosa* are stated to be of the male sex.

In *Erynnia nitida* R.D. (Silvestri, 1910*b*), there is found a very unusual seasonal differentiation in host selection, wherein the larvae of the elm leaf-beetle are attacked by the summer broods of the parasite and only the adult beetles by the last brood. A comparable peculiarity in habit is known in a few species of Hymenoptera, also.

Among the species which deposit their eggs directly upon the body of the host, most are often found to be largely confined to a particular part of the body, rather than placed indiscriminately. Species of a single genus may differ markedly in this respect, even though they attack hosts of the same group which are similar in size, form, and habits. Thus, *Centeter cinerea* (Clausen *et al.*, 1927) places the great bulk of its eggs upon the dorsum of the thorax of the female *P. japonica.* In oviposition, the female parasite normally attacks pairs of beetles *in copula* and dashes diagonally across the thorax of the female, lowering the tip of the abdomen momentarily to deposit the egg thereon. In contrast to this, *C. unicolor* Ald. (L. B. Parker, 1934), which attacks *Anomala* and *Phyllopertha* beetles, places the eggs ventrally on the posterior portion of the abdomen.

Among species attacking caterpillars, the variation in position is also great. Upon free-living caterpillars, either the last two thoracic segments or the last abdominal segments are usually chosen. In the case of *W. quadripustulata*, Allen (1925) states that the thoracic position

upon *Cirphis unipuncta* Haw. is a provision for the protection of the eggs, as a considerable portion of those placed farther back are crushed by the mandibles of the host. The presence of these eggs apparently causes some irritation, which induces the host to attempt to brush them off or to destroy them. A decidedly unusual position for egg placement is that recorded by Ainslie (1910) for *Exorista larvarum* L. upon the larvae of *Hemileuca oliviae* Ckll. The latter is attacked only while in motion and at the moment when the posterior portion of the abdomen is raised, and the egg is invariably placed upon the sole of the "foot," within the crescent of hooklets. Upon the Pentatomidae and other bugs, the tachinid egg may be placed upon the side of the thorax or abdomen, which is the more common habit, on the venter of the prothoracic margin, as in *Gymnosoma fuliginosa* R.D., or on the dorsum or sides of the abdomen while the wings of the host are spread, as in *Phasia crassipennis* L. *Siphona geniculata* DeG. and *S. cristata* F. (Roubaud, 1906), which parasitize tipulid larvae, oviposit upon the stigmatic crown, presumably because this is the only portion of the host body exposed.

The pedicellate egg of *Carcelia gnava* is attached by the tip of the pedicel to a hair of the caterpillar host, whereas in *C. evolans* Wied. (Skaife, 1921*b*) the egg is placed upon one of the thoracic segments of the bagworm host, a position which is obligatory in view of the fact that only that portion of the body is ever extruded from the bag.

In the soil-inhabiting species, the eggs or larvae are deposited upon the surface of the soil, though Davis (1919) states that the female of *Microphthalma disjuncta* Wied. places them in crevices. There is some evidence to show that they are deposited in proximity to host grubs and in considerable numbers at each point, rather than singly. The species that attack hosts in plant stems, such as *Theresia* and *Metagonistylum*, parasites of the sugarcane moth borer, place the larvae near the entrance of the host tunnel, and it is then necessary for them to burrow through the frass that fills the entrance before they reach the host larvae. This habit is common to a great many species which attack hosts that are concealed but that have an open entry hole or later make holes for other purposes in the stems, fruits, or seeds they inhabit.

The female of *Rondanioestrus apivorus* Vill. pounces upon the worker bees while they are in flight but touches the body only lightly and deposits the maggot upon it (Skaife, 1921*a*).

The females of species that deposit macrotype eggs appear to exercise no discrimination in their choice of host individuals for parasitization. This frequently results in individual hosts receiving an excessive number of eggs. A certain portion of these eggs is lost through molting of the host, the proportion varying with the length of the incubation period and the interval between molts of the host. If the incubation period

of the egg is the same as the length of the larval stage of the host, there would be virtually a complete loss of the eggs before hatching, whereas if the egg stage is, for example, three days and the host larval stage six days the loss from this cause would be approximately 50 per cent. There are indications in some species that the early portion of the host stage, immediately after molting, is preferred for oviposition, and in such cases the loss would be much reduced.

There is at times a marked failure in successful parasitization even when oviposition is very extensive. Several authors have pointed out that, toward the end of outbreak periods of the nun moth, *Lymantria monacha* L., in Europe, practically every caterpillar bears tachinid eggs and yet the attack is rarely successful and they develop and emerge normally. It is recorded that a collection of 235 gypsy-moth caterpillars, each bearing 1 to 33 eggs of *Exorista larvarum*, produced only four parasites and that another collection of 252 did not yield a single one. Though only a portion of this loss can be charged to the molting factor, yet it undoubtedly accounts for the loss of a considerable portion of the reproductive capacity of species depositing unincubated eggs upon caterpillars.

A maximum of 228 macrotype tachinid eggs upon one field-collected larva of *Datana minestra* Drury. is recorded by R. L. Webster, and L. S. West mentions a larva of *Samia cecropia* bearing 40 eggs that was still able to attain the adult stage. Tothill *et al.* cite an instance of 72 eggs of *Ptychomyia remota* being deposited upon a single *Levuana* larva, in which only one parasite can develop to maturity. Allen's observations on *Winthemia* indicate that the number of eggs deposited upon different hosts and upon various instars of the same host vary directly with the size of the individuals. The studies of Clausen *et al.* (1933) upon *Centeter cinerea* have indicated that there is no selective oviposition but that the egg distribution follows closely the law of chance occurrence.

The microtype eggs are deposited upon the foliage of the plants that serve as food for the hosts and adhere to the leaf surface by a mucilaginous material that is somewhat soluble in water. In some cases, a particular plant or group of plants serves as the stimulus for oviposition, which is consequently independent of the host itself; in other instances, the attraction seems to be to foliage bearing, or frequented by, host larvae. Dowden has noted that cut leaves, as well as the presence of host larvae, stimulate oviposition by *Zenillia libatrix*, and this simulates the condition that exists while the host larvae are feeding. The eggs of *Racodineura* are deposited upon any plant material upon which earwigs have fed the previous night. In the majority of species, the eggs are deposited on the undersides of the leaves, scattered rather than in groups, and in some species they are placed mainly at the margins. The females

of *Gonia capitata* Deg., a parasite of *Porosagrotis* in North America and Europe, deposit most of their eggs upon the upper sides of the leaves of Graminae, particularly the bluejoint grass, *Agropyron smithii* (Strickland, 1923). The host, however, feeds principally upon the cultivated grains and attacks the bluejoint grass only when other tender vegetation is not available. It also feeds extensively upon alfalfa, but the parasite does not oviposit upon this plant. The value of the parasite is thus greatly restricted, for host larvae upon their preferred food plants are very largely exempt from attack. Nishikawa (1930) mentions that the extent of oviposition of *Gaedia puellae* Nishik. on mulberry foliage is correlated with the infestation of an aleyrodid, *Bemisia myricae* Kuw., upon the secretions of which the female flies feed. The silkworm, which is the principal host of this parasite, does not occur upon mulberry in the field, though species of *Porthesia*, *Acronycta*, and *Bombyx*, some of which are usually present, are what might be termed the "normal" hosts.

Development of the Immature Stages. *Incubation of the Egg, Hatching, and Entry into the Host.*—The range in habit within the family with respect to oviposition, incubation, and hatching of the eggs and the activities of the first-instar larvae incident to entry into the body cavity of the host is as great as in any other group of parasitic insects. The frequent occurrence of partial or complete uterine incubation of the several types of egg produced, which is relatively rare in other dominant groups of parasites, particularly the Hymenoptera, serves as one means of overcoming or circumventing certain of the hazards that might otherwise operate to the disadvantage of the species during a period of external incubation.

The macrotype eggs, in general, undergo the entire embryonic development outside the body of the parent female. There are occasional rare exceptions to this, such as *Ptychomyia remota* (Tothill *et al.*, 1930) in which there is a partial and variable degree of uterine incubation. The normal period of external incubation in this species is 36 to 50 hours; but some eggs have been noted to hatch in 30 minutes, and others have required as long as four days. Among other species in which the incubation period has been determined, it most frequently requires two to three days, with a minimum of one day in a few instances. The eggs of *Eubiomyia calosomae* (Collins and Hood, 1920) are nearly fully incubated at the time of deposition, usually hatching in less than 24 hours, though some hatch in less than three hours.

There are two distinct ways in which hatching and entry into the host body are effected by larvae from macrotype eggs. In *Centeter*, *Meigenia*, and *Trichopoda* and in many other genera that have the indehiscent form of macrotype egg, the larva bores directly downward through the thin chorion on the ventral side of the egg and through the

heavily chitinized integument of the host body. There is, of course, no external evidence to indicate that hatching has taken place. This method is particularly common among those species which attack adult Coleoptera and Hemiptera. Larvae from eggs of this type are usually provided with teeth upon the distal margin of the mouth hook, which serve for rasping purposes (Fig. 210*A*). An exception to this manner of hatching is revealed in *E. calosomae*, in which the young larva escapes from the egg through a hole in the thin ventral chorion; but then, instead of continuing into the host body immediately, it emerges from beneath the egg and effects entry at some other point on the host body.

In the second form, hatching is effected by the lifting of a definite lid, or operculum, at the anterior end of the egg, the fracture taking place along a horizontal line around the front of the egg, somewhat below the median transverse line, and often extending slightly dorsad at each end (Fig. 207*F*). The larva emerges partly from this opening and, with the caudal segments still enclosed within it, braces itself and penetrates the integument immediately in front of the egg. *Phorocera*, *Ernestia*, and *Winthemia* have this habit, and it is probably common among the species attacking caterpillars and other relatively thin-skinned hosts. In some species, the larvae abandon the eggshell altogether and effect entry through the intersegmental membrane or at some other vulnerable point.

Uterine incubation is also partial or complete in the majority of species that deposit microtype eggs, and the entire quota of the female may be present in the uterus and partly or completely incubated before any of them are deposited. These species, among which *Zenillia libatrix* may be mentioned as representative, are consequently able to deposit a large number in a very short period of time. Eggs of this type, whether or not incubated at the time of deposition, are protected from desiccation and mechanical injury by the heavy and variously sculptured chorion, and hatching does not take place until they are ingested by the host larva. In most species, they remain viable for three to five weeks, and N. L. Sakharov records that those of *Gonia ornata* Meig. were still alive two and one-half months after deposition, at which time the caterpillars of the second generation of *Euxoa* were present in the field. The capacity to exist in an inactive condition for such a long period is a marked advantage to the species and offsets, in part at least, the disadvantage of oviposition apart from the host. Townsend cites several genera and species in which the apparently mature eggs in the uterus show very little evidence of embryonic development and they are apparently deposited before this is complete. In these species, ingestion of the eggs by host larvae cannot result in successful parasitization unless the eggs are at least one or two days old.

The manner in which hatching of the microtype eggs takes place has been the subject of considerable difference of opinion. It may be mentioned that the chorion of the ventral side of the egg is thin and membranous as contrasted with thick wall of the dorsum, and this undoubtedly plays a part in hatching. Townsend implies that the action of the digestive juices provides the stimulus for hatching and considers that the heavy chorion serves to protect the embryo from injury by the host mandibles while the egg is being swallowed. This interpretation is questioned by Swezey, who believes that the chorion is cracked by the mandibles of the host, thus permitting the larva to escape. In support of this conclusion, he cites the snapping open of the shell, and the escape of the larva, when pressure is applied to it. Also, hatched larvae were found in abundance in the crop of caterpillars almost immediately after the eggs had been eaten.

More recent observations have been made upon this point by Severin *et al.* (1915), Nishikawa, and Dowden. The first-named authors immersed eggs of *Chaetogaedia* in the fluids ejected from the mouths of *Heliophila* larvae; hatching of some individuals resulted in less than one minute, and 97 per cent hatched within three hours. The same result was secured with the juices of other caterpillars. The presence of these fluids stimulates the larva, and the thin ventral chorion of the egg is broken as a result of its movements. Many eggs hatched when immersed in distilled water for 36 hours, and this was brought about by an increased turgidity of the larva.

There is a very appreciable absorption of fluids by the egg, often resulting in practically doubling its size, and in some species at least the thin ventral chorion bulges out, blister-like, so that the greater part of the body of the larva is enveloped by merely a thin membrane. In consequence, the rupture of the heavy dorsal chorion is unnecessary.

Nishikawa confirms the above general conclusions with respect to *Gaedia*, stating that hatching occurs only after immersion in the digestive juices; he found that a much higher percentage of hatch was secured with a high concentration than with a weak solution. The ventral chorion of the egg is apparently broken by use of the mouth hook. Dowden reports that the mere immersion of the eggs of *Z. libatrix* in the digestive fluids of the host fails to induce hatching but does result in a pronounced swelling which renders them susceptible to rupture due to variation in pressure within the digestive tract of the host. In this species, hatching takes place at any point in the digestive tract, whereas in others it is very largely in the fore-intestine.

The majority of species of the family in which the eggs undergo partial or complete incubation while still within the uterus of the parent produce the membranous type of egg, and in some instances actual

hatching of all eggs in the uterus is not merely occasional but a consistent habit. The female of *Prosena sibirita* never deposits eggs and the eggshells are retained in the "brood pouch," whereas in *Dexia ventralis* they are voided at the time of larviposition. In the latter species, uterine incubation is usually complete, and hatching takes place before larviposition; yet, during periods of extensive reproductive activity by the female, the brood pouch may be emptied before all the eggs are fully incubated, and some of them may require as much as two days' further development before hatching takes place.

Larvae that are deposited externally as such or that arise from the membranous type of egg generally enter the host body through the intersegmental membranes or at some other point where the integument is thin. This is particularly true of the species attacking heavily armored hosts, such as beetles and locusts. In the case of several species, notably *Eubiomyia calosomae*, *Lixophaga diatraeae* Tns., *Siphona cristata*, and *S. geniculata*, it has been asserted that entry is effected through a spiracle. This has appeared logical in the case of *Siphona*, because the egg is deposited upon the stigmatic crown, the only exposed portion of the aquatic host larva. The evidence, however, is not conclusive, and such a mode of entry has not as yet been established as normal in any species. The *Siphona* larva should have no greater difficulty in penetrating the body wall at any other point than is experienced with hosts in air, for the surrounding water presumably presents no obstacles to its activities.

It is recorded by Strickland that many of the planidia of *Bonnetia comta* Fall. are bitten off and killed by the cutworm larva while they are attempting to penetrate the integument, and Muesebeck mentions that brown-tail caterpillars make frantic efforts to destroy or dislodge the larvae of *Sturmia nidicola* Tns. as they bore into the body. This is a mortality factor that does not operate in the case of species having microtype eggs and is comparable to the loss of macrotype eggs through the same agency. The great majority of hosts, however, show no discomfort during the time the maggots are penetrating the body.

The stimuli that attract the planidium type of larvae to their hosts are not well-understood. Many will attach themselves to practically any moving object that comes within reach. Those of *Archytas analis* F. are attracted to many species of caterpillars in which they cannot develop; yet they show no interest whatever in certain other species.

In general, the larvae that find the host and enter its body through their own efforts do so immediately after coming in contact with it. Complete penetration is often effected in less than 15 minutes, though some species often require longer. This variation is probably due mainly to a difference in the thickness and toughness of the integument of the

host. A departure from the above habit is recorded in the case of the planidia of *A. analis* which, when they reach the host, exude a liquid that fastens them horizontally to the skin of the latter, and they may remain in this position for 24 hours or longer before attempting penetration.

The first-instar larva of *Dexia ventralis* Ald. and others of that subfamily, which must search through the soil for their hosts, are of the planidium type, and they penetrate the integument at almost any point as soon as the host is found. Experiments have revealed that the larvae exercise no discrimination among the grubs encountered but that the difference in parasitization of different host species and instars is directly correlated with the thickness and toughness of the integument. Thus, tests under comparable conditions gave a parasitization of only 18 per cent of mature *Anomala* grubs and 85 per cent in second- and early third-instar grubs of *Phyllophaga*. The integument of *Phyllophaga* grubs of these instars is very thin and bare, and, although the initial parasitization was high, the species was not found to develop to maturity in that host.

A very considerable number of species (*Archytas analis*, *Bonnetia comta*, *Ernestia ampelus*, *Eupeleteria magnicornis*, etc.) utilize the eggshell as a cup-like device which serves to anchor the larvae to the substratum while awaiting the coming of a host. The shell is fastened to the leaf or other surface by a mucilaginous material given off by the colleterial glands of the parent female, and it closely envelops the caudal end of the larva (Fig. 208*B*). The larvae of *B. comta* normally stand erect in the shell, even when resting, with the anterior segments retracted, whereas those of *A. analis* (Allen, 1926) lie horizontally on the substratum when at rest. The presence of the collapsed eggshell is not essential to the well-being of the planidia. In both of the above species, they frequently leave the shell entirely under stress of excitement, such as the approach of a host, and they are still able to assume the erect position at will. It does not appear that this adaptation serves any essential purpose in the life of the first-instar larva.

In the great majority of species that inject their membranous eggs directly into the body of the host, rather than depositing them upon or entirely apart from it, the eggs are at least partly incubated in the uterus of the female. A few, however, consistently deposit them before any appreciable embryonic development has taken place.

The pedicellate egg, which is attached to a hair or to the skin of the caterpillar host, hatches very quickly after deposition; and the young larva then seeks out a vulnerable point on the host body at which to make its entry. Its activities thus do not differ appreciably from those of other forms of larvae from membranous eggs except that it is spared the necessity of effecting the initial contact with the host.

Activities of the Larva within the Host.—The various means by which the first-instar larvae of the different types gain entry into the host body have been discussed, and there is, from this point onward, much less diversity in habit than was found during the preceding period in the developmental cycle. That this is so is to be expected, for all larvae now inhabit the same general medium and are subject to the same influences, though the ultimate destination after entry differs considerably among the different types of larva and among species.

The majority of species do not become associated with any particular organ in the host body; yet others have a constant habit in this respect. The organs with which they may be associated are the nerve ganglia, salivary glands, gonads, intestine, muscle fibers, and fat body. The most marked adaptations are found among the microtype larvae, which find their way into the body cavity from the intestine. The young maggot of *Sturmia cilipes* enters one of the nerve ganglia of the silkworm, usually the second to the fifth, and during its stay of about one week in this position causes a pronounced proliferation or enlargement of the ganglion, which also changes in color to white. The occurrence of these larvae in the ganglia brings to mind the same localization of attack by some species of the hymenopterous family Platygasteridae. In *Gonia capitata*, the maggot first remains for a period of 4 to 28 days in the mesenteron of the intestine without feeding, then progresses to the salivary gland, and finally reaches the supra-esophageal ganglion. Several species are known to inhabit the salivary gland throughout this period. *Gaedia puellae*, also a parasite of the silkworm, has this habit and may occasionally be found in the reproductive organs. The period passed within the salivary gland by certain species varies directly with the age of the host larva and may range from 4 to 22 days. The maggot of *Leschenaultia exul* may reach the gland within two hours after ingestion of the eggs by the caterpillar, and it remains there for 8 to 10 days. It lies in the gland itself, rather than in the duct, and a pronounced malformation is produced. The first-instar larva of *Zenillia libatrix* may be found in a muscle, the salivary gland, or occasionally in a histoblast. *S. scutellata* R.D. consistently passes the first stage in a muscle, and its presence results in a marked hypertrophy of the tissue. In *Chaetogaedia monticola,* this period is passed in a sac, apparently formed by an enlarged tracheal tube, near one of the host spiracles. This, however, may be only a respiratory funnel plus a membranous sheath. The first-instar maggots of *Racodineura antiqua* Meig. depart from the usual habit of this group and lie free in the body cavity of the host.

The tachiniform and planidium larvae that gain entry to the host through the body wall, either by direct penetration or by injection by the parent female, are not known to enter nerve ganglia or the salivary gland

at any time. The maggots of *Plagia trepida* Meig. and *P. ruricola* Meig. immediately enter a muscle and pass the entire first stage therein, a habit they have in common with *S. scutellata*, but in these instances the tissue is killed and consequently no enlarged pouch or sac is formed (Thompson, 1915*b*). The larvae of *Rondanioestrus apivorus*, which are parasitic in adult honeybees, feed in the abdomen throughout their developmental period, whereas those of the sarcophagid, *Myiapis angellozi* Seguy, are usually found lodged in the muscles of the thorax (Seguy, 1930). The majority of these species lie free in the body cavity of the host, for the greater part, if not all, of the first stage but a number are intimately associated with the intestine. The young maggot of *Compsilura concinnata* is always found between the peritrophic membrane and the cellular wall of the mid-intestine, and the same is true of *Anetia hyphantriae* Tot. *A. nigripes* and *A. piniariae* Hart. are found in the mid-intestine, often attached to the walls by the spiracular hooks. The young maggot of *Zygobothria nidicola* (Muesebeck, 1922) lies free in the body cavity for 10 to 14 days after penetration and then enters the esophagus, where it lies dormant for about nine months, whereas that of *Archytas analis* remains for a period up to 15 days between the skin and the hypodermal layer before entering the body cavity. The larvae of *Chaetophleps setosa* are often found embedded in the fat body.

Association of certain of the species mentioned with a nerve ganglion, salivary gland, muscle, or the intestine appears to be obligatory, whereas occurrence in a gonad or the fat body, though of frequent occurrence in some species, is believed to be more or less accidental and is not known to be obligatory in any species.

The species that are associated with a definite host organ during their first larval stage usually leave it immediately before or after the first molt, and the great majority then take up a fixed position in the host body for the remainder of the feeding period. This habit relates primarily to respiration and will be discussed under that heading.

It has been pointed out that the first-instar larvae of a considerable number of species, particularly those associated with host organs, pass a long period of time without feeding or apparent growth. Once this begins, however, it is extensive before the molt takes place. This is illustrated in *Zenillia libatrix*, which increases from 0.23 mm. in length to 2.0 mm. before the end of the first stage.

Certain of the free-living species follow a definite migratory course during their period of development in the host body. This is perhaps more constant in the species that have a fixed egg position. *Centeter cinerea* is an excellent illustration of this habit. The egg is deposited upon the dorsum of the thorax of the female beetle, and the young larva bores directly downward into the host body. Initial feeding and the

first molt take place in the thoracic region, and the second instar then enters the abdomen almost immediately after the molt. It gradually works its way to the tip of the abdomen, then turns and reenters the thorax, whereupon the host dies and the second molt takes place. The contents of the thorax are then eaten out, after which the larva again reverses its route and completes feeding in the abdomen. In male hosts, however, the second molt takes place in the abdomen rather than in the thorax.

The first-instar larva of *A. analis* persists in the body of the host caterpillar until the latter transforms to a pupa, whereupon it molts and then takes up a position in a wing pad, in which it produces a characteristic bulge that is readily recognized; the respiratory funnel is formed at this point.

In several species, the larvae are partly or completely enveloped by a membranous sheath which, like the respiratory funnel, is of host origin. It is soft and flexible, of varying thickness, and almost opaque in the species that induce its greatest development. It is apparently the result of a defensive reaction on the part of the host similar to that which occurs where a foreign body is attacked by phagocytes, and thus it differs from funnel formation, which may be considered as the result of a healing process. According to Muesebeck, the sheath of *Sturmia* is made up of hypodermal cells, leucocytes, and compressed fat cells and envelops only the funnel and the posterior portion of the body. In *Siphona cristata* and other species, the young overwintering larva is completely enclosed in the sheath, but in the older individuals the sheath is open at the anterior end. A closed sheath also envelops the young larvae of *Actia diffidens* Curr. and *Winthemia quadripustulata*, which are found in the caterpillar bodies only in midsummer, and consequently the sheath must be permeable to the blood of the host, from which the larvae derive their nourishment.

As is the case with many other parasitic groups, the death of the host does not necessarily take place in the same stage as that which is originally attacked. Among lepidopterous hosts, initial attack invariably is upon the larvae, usually when they are half-grown or larger. In the majority of host species, death does occur in that same stage, but a considerable number consistently attain the pupal stage. A few tachinid species are indiscriminate in this respect, and the stage at which the host is killed depends upon the age of the larvae when parasitized. Many Tachinidae kill the host relatively early with respect to their own stage of development, often when they are in the second stage, and death is followed by a more or less complete liquefaction of the body contents. This condition is quite distinct from that brought about by putrefaction. *Cirphis unipuncta* caterpillars parasitized by *Winthemia* die two days

after penetration by the parasite larvae; yet the latter are still able to develop to maturity.

The death of worker bees parasitized by *Rondanioestrus apivorus* takes place very suddenly; often, they are stricken while in full flight, fall to the ground, and die within a few minutes. The mature larva emerges from the body within 10 minutes thereafter. In view of the continued activity of the affected bees until the parasite larvae are mature, it is probable that the latter feed only upon the body fluids and that, when ready to emerge, they cut the nerve cord and thus bring about almost instantaneous death.

The manner of emergence of the mature larva from the host body presents several variations, depending on the stage of the host and whether or not the host is alive at this time. In larval hosts, the mature maggots usually make an incision in the ventral area of the host abdomen, at which point the integument is thinnest. Some authors assert that this is accomplished by use of the mouth hooks, but others state that it is brought about by pressure of the caudal end, aided by the solvent action of the body secretions. Nielsen (1909) describes the emergence of the maggot of *Bessa selecta* Meig. hind end foremost, in this way. In *Microphthalma michiganensis* Tns., a parasite of scarabaeid grubs that has been studied by Petch and Hammond (1926), "a large opening is dissolved away in the body wall of the grub to allow the exit of the parasite, which exposes the caudal end of the body first." The first-mentioned is believed to be the more normal habit. The aperture may be made some time prior to actual emergence and may be utilized in the meantime for respiratory purposes. Emergence from lepidopterous pupae is usually effected at some point on the venter of the body, and at times from the wing pads.

Among the hemipterous hosts, many species are still alive at the time of emergence of the mature tachinid maggots. In the cases of *Nezara* and *Anasa* parasitized by *Trichopoda pennipes*, *Eurygaster* by *Clytiomyia*, and *Dysdercus* by *Alophora* and *Catharosia*, the maggots leave the body through the anal opening or through the intersegmental membrane near by, and the host does not die until several days later. A similar condition is occasionally found among adult coleopterous hosts. The maggot of *Minella chalybeata* Meig. effects its emergence from the chrysomilid beetle, *Cassida deflorata* Suffr., through an aperture dorsally between the first and second abdominal segments; and, as the vital organs are not affected, the host does not die until some time later. The death of parasitized earwigs also follows, rather than precedes, parasite emergence from the body, and the maggots make their way out through the intersegmental membranes near the posterior end of the abdomen.

The maggot of *Thrixion* emerges from the body of its phasmid host through the wound at the side of the thorax which had previously been utilized for respiratory purposes, and consequently the mechanical injury that is inflicted at this time is relatively slight.

A few species, such as *Zenillia pexops* B.B., that attack larval hosts in exposed positions pass the winter in the mature larval stage within the dry host skins. They are consequently exposed to sudden changes in both temperature and humidity of great extent and must adapt themselves to such conditions. These larvae are golden-yellow in color, owing to large quantities of fatty materials stored within the body, and the skin is much heavier than in species not exposed to the same adverse influences.

It has generally been assumed that the Tachinidae consistently have only three larval instars, though Petch and Hammond state that there are four and possibly five in *Microphthalma michiganensis*. Undoubtedly the great majority have only three feeding stages, though several authors have indicated the possibility of a fourth in the microtype larvae, due to the early stage in embryonic development at which hatching takes place.

In *Actia diffidens*, *Paradexodes epilachnae*, and several other species that have been studied in some detail, it has been noted that the inner wall of the puparium is lined with a distinct transparent membrane which has been determined to be a true cast skin, discarded after a short but definite prepupal stage. Further investigation will probably reveal the general occurrence of this prepupal instar in the family.

Pupation.—The place of pupation of the Tachinidae is quite variable, particularly among species that develop in lepidopterous hosts. The majority form the puparium outside the body of the host; those from free-living caterpillars usually enter the soil, whereas others that develop in stalk borers, leaf rollers, etc., generally pupate within the burrow or leaf roll. A few species, such as *Voria ruralis* Fall., *Sturmia nidicola*, and *Echinomyia fera*, pupate in the host larval skin. If the parasite is solitary, the puparium is oriented the same way as the host; if the parasites are gregarious, the puparia lie transversely in an even row. Those species which reach maturity in the host pupa often form the puparium within the pupal shell. In the case of attack upon sawfly larvae, pupation may take place either within the larval skin or in the soil.

The few records available regarding the pupation habits of Tachinidae attacking coleopterous larvae indicate that this frequently occurs within the larval skin. When adult beetles serve as hosts, the greater number of species pupate within the abdomen of the dead beetles, with the head at the posterior end of the abdomen, thus facilitating emergence. This is particularly true of the solitary species such as *Centeter*, *Hamaxia*,

Erynnia, and *Trophops*. Certain of the gregarious species likewise pupate in the host body, notably *Palpostoma subsessilis*, of which as many as 28 develop in one beetle, and *Cryptomeigenia theutis*. In *Eubiomyia calosomae*, which may produce up to 16 individuals in a single *Calosoma* beetle, about 40 per cent pupate within the host abdomen, and the remainder do so externally in the space between the abdomen and the elytra. Several solitary species emerge from the host beetles for pupation, among which are *Degeeria funebris* Meig. and *Minella chalybeata*. The mature larva of *Chaetophleps* emerges from its dead or dying chrysomelid host through an incision at the juncture of the head and thorax and pupates in the soil near by.

The general habit of species having hemipterous hosts is to emerge from the body and pupate in the soil. In *Trichopoda pennipes*, however, the summer generation pupates in the soil whereas the puparia of the overwintering brood are found in the dead bodies of the hosts.

The species attacking earwigs pupate outside the body of the host, as do also the few species having dipterous hosts. The mature larvae of *Dexia*, *Prosena* and other white-grub parasites leave the body and pupate in the soil 2 to 4 cm. beneath the host remains.

Thompson (1910) has shown that it is the normal habit of dipterous larvae which enter the soil for pupation to reverse their position so that when the puparium is formed the head end points upward. The emerging fly, by the use of the ptilinum and the backwardly directed spines of the body, is able to force its way through the soil, but only forward, and the above-mentioned position of the puparium in the soil directs the activities of the emerging adult toward the surface. In his observations upon *Paradexodes*, Landis found that in 46 per cent of the pupae the head end was directed upward, in 29 per cent it was directed downward, and in 25 per cent the pupae were lying in a horizontal position.

It has been pointed out that gregarious species, when pupating within the skin of a larval host, often take up a regular transverse position. Those which pupate outside the host body are usually scattered, or they may be closely packed but without definite order. A conspicuous exception to this occurs in *Sturmia cubaecola* Jaenn. and *S. protoparcis* Tns. (Greene, 1921) in which the several dozen puparia from a single host are cemented together in an upright position to form a disk-like mass.

The general effect of changes in temperature and humidity upon the pupae varies markedly among species. Those which pupate in the soil are protected to a considerable degree from sudden changes and are not able to withstand prolonged exposure to temperatures or humidities differing greatly from those experienced under natural conditions. The most resistant forms are those which pupate above ground and pass

the winter in the pupal stage. These withstand wide fluctuations in both temperature and humidity. With insectary material, a maximum emergence is secured from species pupating aboveground when they are held under comparatively low humidities, whereas with the majority of soil-inhabiting forms an almost saturated atmosphere is most favorable for development. Grösswald (1934) reports that maximum emergence from puparia of *Parasetigena segregata* Rond. was secured from material which had been stored at a temperature of 7°C. and 100 per cent relative humidity. Hefley's (1928) experiments upon *W. quadripustulata* resulted in 33.4 per cent emergence at 7.1 per cent humidity and 100 per cent emergence at humidities of 73 to 100 per cent. The viability of puparia of both the summer and the winter broods is directly proportional to the atmospheric humidity up to 73 per cent, above which it remains at 100 per cent. In contrast to this, the emergence of host adults from healthy pupae that are also found in the soil is inversely proportional to the humidity. Thus, optimum conditions for the host are disadvantageous to the parasite, and vice versa. The duration of the pupal stage of the parásite is also appreciably influenced by changes in humidity; at 27°C., this ranges from 26.3 days at 7.1 per cent to 15.7 days at 73 per cent and then lengthens to 20 days at 100 per cent.

Respiration of Larvae and Pupae.—The oxygen requirements of the larvae within the host body are met by cutaneous respiration, by temporary tapping of an air sac or tracheal branch of the host, or by the establishment of a fixed source of exchange with the outside air through the host tracheal system or directly through the integument. This latter adaptation involves the formation of a respiratory funnel within which the caudal end of the body of the parasite larva, with the posterior spiracles, is enclosed.

Cutaneous respiration is the only way in which the young larvae embedded in muscular tissue, a salivary gland, or a ganglion are able to secure their oxygen requirements. As growth proceeds, this source probably proves inadequate, and as a consequence of the greater need their position in the body of the host is changed so that direct access to a source of supply is secured.

A considerable number of species that are free-living in the body of the host have posterior spiracles equipped with sharp, heavily chitinized hooks, and these are used to puncture an air sac or tracheal branch. This adaptation, which is particularly common among the parasites of adult beetles, permits free movement, for the connection is only temporary. Many of these larvae persist in the free condition throughout the larval period, though the spiracular hooks may be lacking in the later instars. In *Anetia* spp., the spiracular hooks are present on the first-instar larva, whereas in *Centeter* spp. and *Hamaxia incongrua* they are

borne only by the second instar. In *Centeter*, they are employed to puncture an air sac to provide for respiratory needs, whereas in *Anetia piniariae* and *Compsilura concinnata* they not only fulfill this purpose but serve to hold the larva in a definite feeding position.

The larval respiratory funnel, in which the posterior end of the body, with the functional spiracles, is fixed, is an adaptation of very general occurrence in the Tachinidae; but, strangely enough, it is found elsewhere in only a very few highly specialized parasitic species of the closely related Sarcophagidae and in no other families of parasitic Diptera. The only instance of the development of an apparently similar relationship elsewhere is found in the chalcidoid family Eucharidae, of which two species of *Orasema* are internal parasites of larvae (see page 227).

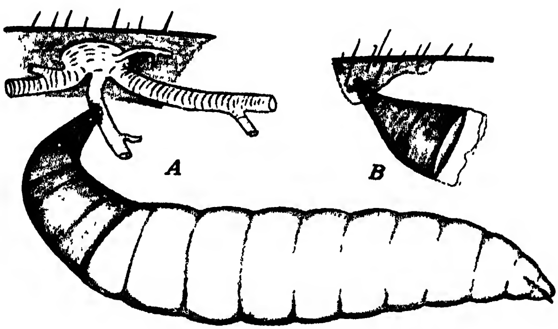


FIG. 204.—The points of formation of the larval respiratory funnels of Tachinidae. *A*, a larva of ***Prosena sibirita*** F. with the funnel arising from a tracheal branch near a spiracle; *B*, the funnel of ***Dexia ventralis*** Ald. arising from the puncture in the host skin through which the first-instar larva entered the body. (*From Clausen et al.*, 1927.)

The funnels of the Tachinidae may be integumentary in origin, giving direct access to the outside air, and formed at the point of entry of the young larvae or at some other point by a larva that has already passed a period of free life in the host body, or they may be of tracheal origin, usually arising upon one of the main lateral trunks or on a spiracular stalk, but occasionally upon a tracheal branch or air sac.

Pantel distinguishes two classes of respiratory funnels, based upon the manner of origin. Those which develop at the point of entry of the parasite larva into the host body are designated as primary and are always integumentary, whereas others which arise as a result of the activities of the larva from within the body are secondary. The latter may be either integumentary or tracheal in origin. There is, however, no essential difference in form or function between the two classes.

The stage in larval development at which the respiratory connection, with the formation of the funnel, is made is exceedingly variable. In a considerable number of species, it takes place at the time of initial

entry into the host body, and funnel formation can often be readily distinguished within a few hours after penetration. Species inhabiting lepidopterous hosts that have this habit are *Bonnetia comta, Ernestia ampelus, Phorocera agilis, Ptychomyia remota, Sturmia inconspicua* Meig., *Winthemia quadripustulata,* etc. The earwig parasite, *Bigonicheta setipennis,* and *Dexia ventralis* (Fig. 204*B*) in scarabaeid grubs likewise fix themselves at the point of entry. This immediate formation of the funnel at the point of entry of the parasite is of rare occurrence in hosts that are in the adult stage when attacked.

The position of the funnels, when formed at the point of entry, is often relatively consistent for a given species. The planidium of *Bonnetia comta* usually penetrates the skin of its noctuid caterpillar host on the dorsum of the first thoracic segment, and *Bigonicheta* does so in the intersegmental areas of the thorax. In these instances, the location of the funnel is a matter of choice on the part of the planidium, but in the species that deposit macrotype eggs it is governed by the location of the egg on the host body. In *Winthemia* and some others that have the dehiscent form of egg, the larva remains with its posterior end in the eggshell while penetration is being effected, and the funnel is consequently found immediately in front of the egg.

Among the species that make the respiratory attachment after a period of free life in the host body or of confinement in a definite organ, it may be either with the integument or with the tracheal system. The records available indicate an approximately equal division between the two points of attachment. Among the species having caterpillar hosts, *Actia diffidens* Curr. (Prebble, 1935) is invariably found in an integumentary funnel on the mesothorax, whereas *Sturmia nidicola* and *Leschenaultia exul* are located in the posterior region of the abdomen. *Archytas analis* and *Gonia capitata,* which form the funnel only after the host has reached the pupal stage, are situated in a wing pad, whereas *Zenillia libatrix* selects a point between any of the ventral plates of the head sclerites.

Of the species that make their attachment to the tracheal system, *Compsilura concinnata* and *S. cilipes* do so with the short stalk leading from a spiracle to the main longitudinal trunk, often so close to the spiracle as to be considered directly connected with it. The greater number make their attachment to the longitudinal trunk itself, but near the base of a spiracular stalk, and in caterpillars and coleopterous larvae a spiracular stalk in the first or second abdominal segment is the favored location (Fig. 204*A*). In *Zenillia roseanae* B.B., the connection is with one of the smaller tracheal branches permeating the fat body of the *Pyrausta* larva, whereas the funnel of *Eubiomyia calosomae* is formed on a tracheal branch in the metathorax of the beetle host. Matthey (1924)

records an unusual adaptation in *Exorista larvarum* L. in which occasional larvae are found to have broken the longitudinal tracheal trunk of the host and to have utilized the broken end of the trunk itself as a funnel enveloping the posterior portions of the body. *Gymnosoma rotundatum* L., which is parasitic in Pentatomidae, makes its connection, during the intermediate larval period, with one of the air sacs in the thorax.

The species that make the respiratory connection with the tracheal system seldom reveal any external evidence of their presence until near the end of the feeding period. If the funnel is formed close to a spiracle, it may at times be visible. The integumentary funnels, however, are usually visible almost immediately after the connection is made, not only because of the actual perforation but by the dark-colored funnel showing through the host skin if this is relatively thin and not heavily sclerotized.

The tracheal funnel represents a defensive reaction on the part of the host to the irritation incident to the making of the perforation in the integument or the tracheal wall by the parasite and to the persistence of the posterior end of the body of the latter in the wound. According to Prell, it is a wound-scab formation; if this is true, its make-up should be constant whether it arises from the integument or a trachea. Tothill states that the tracheal funnel of *Compsilura* consists of an inner chitinous layer, a median hypodermal layer, and an outer basement membrane.

There is a wide variation in size and form of the funnel, both among species and among the different parasite instars. It is quite short, flat, and almost button-like in *Thrixion* (Pantel, 1898), parasitic in Phasmidae; but in the great majority of cases it is cup-like and closely envelopes several of the posterior segments of the parasite body. It increases gradually in size with the growth of the larva, and the basal portion may eventually appear as a more or less slender stalk. Usually the funnel is greatly darkened in color, this being most pronounced near the point of attachment, where the wall is thickest, and fades out toward the rim. In a very few species, the funnel is almost colorless. Occasionally, it has a distinctly "segmented" appearance due to a marked difference in size and form to accommodate the successive instars.

The parasite larva may undergo one or both of its molts during the period of its connection with the funnel, and when this takes place the exuviae remain as a somewhat crinkled lining on the inner wall of the funnel instead of being matted into its base, where they would interfere with respiration. Baer (1921) states that the first exuviae are more frequently ejected from the mouth of the funnel. This is quite possible in the species that form the funnel at the point of entry, for the perforation is often relatively large. An usual manner of molting is found in *Anetia nigripes*, the first-instar larva of which lies in the mid-gut of the

caterpillar host. A transverse split takes place just above the caudal spiracles, and the skin is then cast off over the head.

At the time of molting by the host, the union between the funnel and the integument is broken, and consequently no interruption of function or injury to the parasite larva occurs. Several instances have been noted, however, in which the funnels of first-instar larvae have been pulled out of the wound as the skin was cast. The larvae, however, remained *in situ*, with the posterior portion of the body extruded from the wound, and they had no difficulty in forming new funnels at the same point.

The manner in which the formation of the respiratory funnel is induced by the parasitic larva has drawn the attention of several investigators. Tothill has assumed, in the case of *Compsilura*, that the initial perforation in the tracheal tube is made by the mouth hooks of the larva. Pantel emphasizes, however, that in *Thrixion* and various other species this is accomplished by the use of the posterior end of the body, and various later authors have corroborated this conclusion. Landis (1940) has recently observed the manner in which perforation of the integument is accomplished by the third-instar larva of *Paradexodes epilachnae* in the body of the larva of *Epilachna varivestris* Muls. In its early third stage, the parasite larva frequently abandons the funnel that it has utilized up to that time and makes a final respiratory opening on the dorsum of the host body. To accomplish this, the kidney-shaped spiracular plates are flexed against the inner side of the integument until it is cleared of muscular and other tissue. They are then pressed closely to the surface, and a partial vacuum is created, which causes the integument to come into close contact with the serrate edges of the plates, and the rasping action of these plates finally results in perforation at that point.

In general, a single respiratory attachment is made during the life of the larva, and its position remains fixed in the host body from the time of formation of the funnel until it is abandoned for gross feeding in the third stage. This is not an invariable rule, however, and *Archytas analis*, which occupies a funnel in the wing pad of the host pupa, leaves this one in the early third stage and makes a second breathing pore in the head or anterior thoracic region. In *Paradexodes*, the initial funnel, arising from a spiracular stalk, is formed at the end of the first stage, and this is abandoned at the second molt and attachment made to another spiracular stalk. This second funnel is for a portion of the stage only, following which a third opening is made, this time in the integument, or the larva may even enter the intestine and lie at either end, utilizing the natural openings of the host for respiration.

The instances that have been cited show that the initial funnel formation may take place immediately after entry into the host body or

during a later stage of larval development, and the time at which this is done is relatively constant for any given species. In the majority of species, it is during the first stage, but it takes place only after the first molt in *Gonia capitata*, *Leschenaultia exul*, and *Zenillia roseanae*. There is a small group of species that are said not to make a definite attachment or to induce the formation of a respiratory funnel at any time. Among these may be mentioned *Anetia nigripes* and *A. piniariae*, which are parasitic in caterpillars, *Centerer cinerea*, *Hamaxia incongrua*, and *Palpostoma subsessilis* in adult Scarabaeidae, *Doryphorophaga* in chrysomelid larvae, *Dexia rustica* F. in scarabaeid grubs (Boas, 1893), *Trichopoda pennipes* in adult Pentatomidae, and *Fortisia foeda* Meig. in *Lithobius*. With respect to a number of species that have been studied only superficially, it has been asserted that the larva is free-living within the body merely because the funnel is not visible externally. Even in thin-skinned hosts, the funnel of some species, such as *Prosena sibirita*, cannot be detected by external examination, and in others it is very delicate. A closer examination will probably show that some of these species do establish a definite connection with the internal tracheal system.

It has been pointed out that cutaneous respiration is normal in the first larval stage of many species, particularly those inhabiting one of the organs of the host, and spiracles are lacking in *Racodineura* and several other species. Those which are free-living throughout the larval period secure their air supply, during the later stages, largely by means of frequent temporary connections with an air sac or a tracheal branch.

The time at which the connection with the respiratory funnel is broken varies with the species concerned and with the physical condition of the host. The determining factor is probably whether or not the larva can reach its source of food during this period. In *Degeeria luctuosa* Meig. parasitic in *Haltica* beetles, the connection is maintained until the end of the third stage; this is possible because the attachment is to a tracheal trunk near an abdominal spiracle and all organs of the abdomen, upon which the maggot feeds, are within reach. In contrast to this, the larva of *Eubiomyia calosomae* is attached to a tracheal branch in the metathoracic region; consequently, to complete its feeding, the connection is broken very early in the third stage, and thereafter it wanders free in the body of the living host. The persistence of the respiratory connection reaches its extreme in the case of *Siphona geniculata*, in which the larvae at times maintain their connection with the funnel even after emergence from the host body (Rennie and Sutherland, 1920).

Several other adaptations in habit relating to respiration are known. In *A. piniariae*, the young larva of which inhabits the mid-gut of the

host, the resumption of feeding in the spring is marked by the cutting of two openings in the intestinal wall; one of these is near the head, for feeding purposes, and the caudal spiracles are thrust through the second opening. In this position, many tracheal branches are held by the spiracular hooks, and the air supply is derived from them. The mature larvae of *Ginglymyia acrirostris* Tns. (Lloyd, 1919), which are found in the aquatic larvae of *Elophila fulicalis* Clem., extrude the large stalked spiracles completely through the dorsal integument of the host (Fig. 205). Just prior to pupation, the host replaces its thin, web-like covering

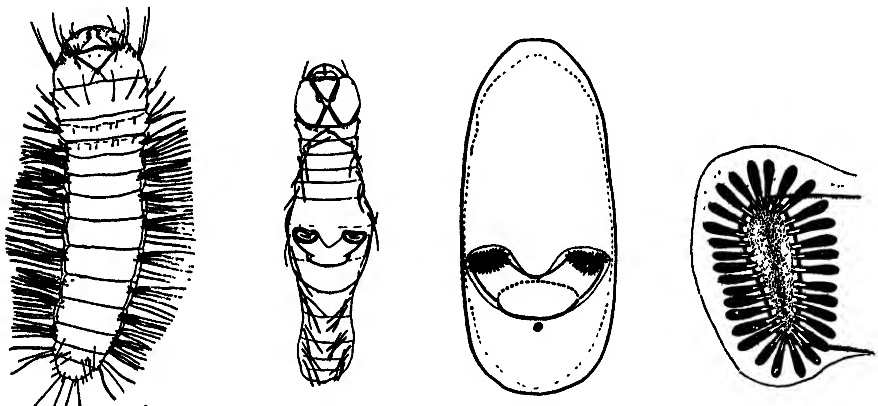


FIG. 205.—*Ginglymyia acrirostris* Tns. *A*, an unparasitized larva of the host, *Elophila fulicalis* Clem.; *B*, a parasitized larva of *Elophila* showing the extruded spiracles of a third-instar larva of *Ginglymyia; C*, a puparium within the host remains, with the spiracular stalks extruded; *D*, a posterior spiracle of the puparium. (*From Lloyd*, 1919.)

with a heavy, oval, roof-like structure, constituting the cocoon, which has a number of openings at each end. The water passes freely beneath this covering, and a large bubble of air forms at its center. The forked spiracular structure of the parasite extends from the middle region of the host body into this bubble, and thus the mature larva and pupa are able to secure an adequate supply of air. It is interesting to speculate on the manner in which this adaptation may have arisen; transitional forms are not known, and these presumably would not fulfill the requirements. It is probable that the parasite has adapted itself concurrently with the host, for the latter is one of the very few species of the order that has adopted an aquatic mode of life.

A further respiratory adaptation is found in the first-instar larva of *Plagia trepida* (Thompson, 1915*b*) which bears a well-developed anal vesicle in the form of a large plate occupying the greater portion of the ventral surface of the last segment and in the center of which the anal opening is situated. This vesicle is formed of large cells having a

resemblance to the striate wall of the middle intestine. This larva normally lies in a dead host muscle, and the great development of the vesicle is in response to the need for oxygen, which is not available directly. Other larvae confined to host organs are bathed in copious secretions, resulting partly from the hypertrophy of the parts involved, and consequently the need for respiratory adaptations is not so great. Pantel first suggested a respiratory purpose for this structure in the Tachinidae. It is not known to occur in any genus of the family except *Plagia* but is present in bilobed form in the Conopidae. Essentially, this structure appears to be homologous with the anal vesicle of various parasitic Hymenoptera, where it reaches its highest development.

Little attention has been given to the respiration of tachinid pupae. It is evident that the spiracles of the puparium, representing those of the third-larvae exuviae, are not utilized directly, for there is no connection with them. The species having extruded prothoracic cornicles may secure their air supply from the outside, but the extensive development of the internal spiracles in all species would indicate that these are the principal organs serving this purpose. Where the cornicles do not penetrate the puparial wall, the larval spiracles may remain sufficiently open to permit of the passage of air into the general cavity of the puparium. In his studies on *Rhagoletis pomonella* Walsh, Snodgrass (1924) concluded that the anterior larval spiracles provide the channels through which air enters the puparial chamber. At the time of the molt, the tracheal branch or stalk that leads to the spiracle is pulled out of the body, and it remains distended, though invariably broken, on the inside of the puparial shell. The same adaptation may well occur in the Tachinidae.

Emergence of the Adults.—Emergence of the adult fly from the puparium is effected by the expansion of the ptilinum, which forces off the two parts of the operculum, and the fly then works its way out. Penetration of soil or other material is accomplished by alternate expansion and retraction of the ptilinum, aided by the backwardly directed spines of the head and thorax, and by the use of the legs.

The manner of emergence of the adult flies from puparia still enclosed within host cocoons or burrows has been the subject of considerable speculation. Where the puparium is contained within the dead host skin, this is usually thoroughly dried and closely adherent to the outer surface of the puparium and is broken by the outward pressure of the expanding ptilinum. In dead beetles upon or in the soil, the intersegmental membranes of the abdomen are so thin and weakened by decay that the fly has no difficulty in forcing the segments apart.

The cocoons of Lepidoptera and Tenthredinidae present a markedly different problem, for the walls, composed of varying quantities of silk

in addition to other material, are often too tough and heavy to be broken by pressure alone. Robbins (1927) has determined the manner in which emergence is accomplished by *Diplostichus janitrix* Htg. from the cocoons of *Diprion pini* L. After completion of feeding in the body of the host, the parasite maggot emerges therefrom and prepares for its later exit by cutting a circular groove with its mouth hooks around the inner wall of the cocoon at one end. When the fly emerges from the puparium, it forces off this cap, which is only lightly attached by the outer silken layer. Cocoons containing unparasitized sawfly larvae do not show this inner groove, and adult-sawfly emergence is accomplished by cutting away a cap, which is somewhat larger than that removed by *Diplostichus*, with the mandibles. This subject had previously been studied by Prell (1924), and his general conclusions were corroborated by Robbins. De Fluiter (1932, '33) has recently investigated this matter more fully and found that the parasite may emerge from either end of the host cocoon, thus establishing definitely that the cap structure is related solely to the parasite. The great majority, however, do emerge from the anterior end.

Tachinid parasitization of lepidopterous species is common even among those which form the heaviest walled cocoons. *Chaetexorista javana* apparently experiences no difficulty in emerging from the egg-like cocoons of *Monema flavescens*, which are exceedingly hard and tough and can be cut with a knife only with some difficulty. The cap, which is normally forced off by the host itself, is likewise removed by the parasite. The circular line of union of the cap with the remainder of the cocoon is comparatively weak, and an oral secretion may serve to soften the lining sufficiently so that the pressure the fly is able to exert causes it to break away. Some Lepidoptera that spin silken cocoons leave a distinct opening or loosely woven area at the anterior end of the cocoon, through which the parasite larva or adult is able to emerge without difficulty. That difficulty in emergence is experienced with some hosts is demonstrated in the case of *Winthemia datanae* Tns. when parasitic upon *Samia cecropia*. The larvae are apparently unable to penetrate the wall of the cocoon, and they die from desiccation even before pupation can be accomplished.

The Life Cycle.—The duration of the life cycle of the Tachinidae, from egg to adult, ranges from a minimum of 10 days, in the case of *Metagonistylum minense* under tropical conditions, to the annual cycle of many species. The great majority of multibrooded species complete the cycle of the summer broods in three to four weeks. The incubation period is markedly variable; for many species are larviparous or ovoviviparous, and the microtype eggs, though fully incubated at the time of deposition, must be eaten by the host before hatching can take place and in some

species are known to remain viable for as long as two and one-half months. The unincubated macrotype eggs hatch in 2 to 4 days. Free-living larvae, which need to await the approach of a host or must search for it, are able to survive for a considerable period, up to 10 days in the case of *Ernestia ampelus*.

The larval feeding period of summer broods is very short in some cases, being only 4 to 6 days in *W. quadripustulata*, 7 days in *Lixophaga*, and 6 to 8 days in *Centeter* spp. In general, however, 12 to 16 days may be considered as the more frequent feeding period for the summer broods. In *Bigonicheta*, however, this period is exceedingly variable, ranging from 21 to 90 days, its duration being dependent upon the amount of food material available in the body of the individual hosts (Mote *et al.*, 1931). In contrast to this, the developmental period of the larva of *Paradexodes epilachnae* is not similarly affected, and the duration of the feeding period is the same, whether in young or mature larvae, prepupae or pupae.

The pupal period of summer-developing broods ranges from 5 to 7 days in *Hyalomya aldrichi* to 25 to 30 days in *Sturmia nidicola*, with 8 to 12 days as a general average for the family. Dowden has pointed out that the pupal stage of the females of *Zenillia libatrix* is 1 or 2 days longer than that of the males, and it is quite probable that this difference between the sexes is general.

Hibernation of the Tachinidae takes place mainly in the pupal stage, though there are a number of departures from this habit. The next most common habit is in an early larval stage within the living-host larvae or pupae, and this occurs commonly in lepidopterous hosts. Of the Dexiinae, the single-brooded *Prosena sibirita* is in the first stage within the host grub, whereas *Dexia ventralis* and *Microphthalma* are in the second stage during that period. The species attacking adult beetles that persist through the winter are usually in the early larval stage within the body. Species of *Erynnia*, *Chaetophleps*, *Degeeria*, *Eubiomyia*, and *Stomatomyia* have this habit. A number of species of *Winthemia* hibernate in the mature larval stage in the soil. *Zenillia pexops* (Wardle, 1914), which develops in sawfly larvae, passes the winter in its mature larval stage within the dried skin of the host, and a few other species are known to have the same habit. The hibernation habits of a considerable number of North American species are recorded by Schaffner and Griswold (1934). It has not been conclusively established that any species passes the winter in the adult stage in temperate regions, though the available evidence points to that habit in the case of *Hamaxia incongrua* in Japan and Chosen.

Normal hibernation in the pupal stage is most often a direct result of low temperatures, but this is not the only factor responsible for the prolongation of this stage. A considerable number of species pass into

a state of diapause irrespective of prevailing temperatures; in some instances, this can be broken prematurely by subjecting the pupae to a period of pronounced cold. The observations by Thompson (1928) on *Bigonicheta setipennis* are of particular interest. This species appears to have two types of puparia; in one, the fly develops and emerges rapidly, whereas the second persists until the following spring, when the adult flies appear. Emergence of the first form cannot be indefinitely retarded by low temperatures, nor can that of the second type be forced by high temperatures. This is considered to be "an inherent difference of a profound physiological order." According to Pantel, the two types of pupae are found most commonly in species restricted to a single host or to a very small number of hosts and is an adaptation advantageous to the parasite in that it increases the opportunities of the brood for finding hosts, inasmuch as a portion emerge during the autumn and the remainder the following spring. This adaptation is known to occur in several other orders, including parasitic groups, and may take place in either the mature larval or the pupal stages.

The number of generations produced each year ranges from 1 in a considerable number of species occurring in temperate regions to 8 to 10 in *Lixophaga* (Scaramuzza, 1930) and *Prosopaea indica* Curr. in the tropics. In *Metagonistylum*, the number is probably considerably higher, for host stages suitable foı parasitization are available throughout the year, and there is no period of hibernation or estivation.

The species that are parasitic in adult chrysomelid beetles and Pentatomidae often have a considerably greater number of generations each year than do the hosts. This applies particularly to those which pass the winter in an early larval stage in the hibernating hosts. *Degeeria luctuosa* has this habit and completes its development sufficiently early in the spring to produce an additional generation upon the hibernating brood of beetles. *Chaetophleps setosa* regularly passes through five generations annually under the temperature conditions that prevail in Illinois. *Clytiomyia helluo* F. completes four generations, and at times five or six, in *Eurygaster*, which has an annual cycle (Jourdan, 1935).

In the great majority of species, the seasonal cycle of the parasite is correlated with that of the preferred host, but in a number of instances there is an obligatory alternation of hosts. This occurs particularly among multibrooded species that pass the winter in the early larval stages in the bodies of the living hosts. Thus, a species having this habit would be unable to exist solely upon a host species that hibernates in the egg stage. *Compsilura concinnata* is one of this group. The gypsy moth is a favored host, but the parasite would be unable to persist upon it alone. An exceptional adaptation to bridge the winter period has been developed in *Erynnia nitida*, a parasite of the elm leaf-beetle.

The two summer generations develop in the larvae whereas the overwintering brood develops in the hibernating beetles (Silvestri, 1910).

The seasonal cycle of *Dexia ventralis* is of interest because of an unusual alternation of hosts (Clausen *et al.*, 1927). This species is a solitary internal parasite of the grubs of a series of Scarabaeidae in Asia. Under field conditions in Chosen, there are normally three generations each year (Fig. 205). The larvae produced by the spring brood of females attack the grubs of *Popillia* spp., the second generation occurs in *Serica* spp., and the overwintering generation in *Miridiba koreana* N. & K. Thus, the successive generations during the season develop each upon a different scarabaeid subfamily. A portion of the population,

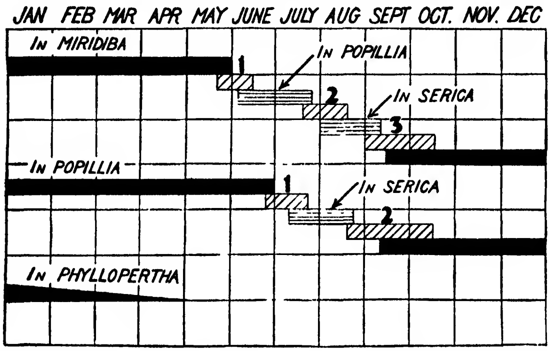


FIG. 206.—The seasonal cycle and alternation of hosts of *Dexia ventralis* Ald. in Chosen. The numbers refer to the successive broods of adults of the parasite, the heavy black bars represent the overwintering host grubs, and the horizontally ruled blocks the summer host grubs. (*From Clausen et al.*, 1933.)

however, has only two generations annually, and in this instance the overwintering host is *P. castanoptera* Hope, rather than *Miridiba*. The grubs of *Popillia* attain the pupal stage approximately one month later than does *Miridiba*, and *Dexia* development is delayed correspondingly, so that the following generation is directly upon *Serica*, the intervening one on *Popillia* being omitted. A considerable adaptability is thus evidenced by the parasite, but the complexity of the annual cycle and the host preferences indicate that the species requires at least one alternate host in order to attain numerical abundance. The adults appear in the field at about the time of appearance of the adult beetles of the host brood upon which they had developed; consequently, with a single host having a strictly annual cycle, only first-instar grubs would be available for attack for a considerable period. This makes it more difficult for the planidia to locate them in the soil, and they are not in a suitable physical condition for extensive parasitization. It is therefore questionable whether the species would be able to maintain itself upon a single host species unless the latter has at least a partial two-year cycle, as a result

of which grubs in a stage of development suitable for parasitization would be available at all times.

Sex Ratio and Parthenogenesis.—Few definite data are available regarding the sex ratios of the Tachinidae, and the lack of observations upon this point can probably be attributed to the difficulty of distinguishing between the sexes by mere superficial examination. E. S. Gourlay mentions that the single brooded *Hystricina lupina* Swed. of New Zealand shows a preponderance of females in the ratio of 4 to 1. In *Paradexodes*, approximately equal numbers of the two sexes are recorded, with a tendency toward a higher ratio of females at higher temperatures.

The only instance in which parthenogenetic reproduction has been claimed to occur is in *G. puellae* (Nishikawa, 1930). It is stated that unfertilized females deposit a few eggs, usually less than 10, in contrast to the several thousand produced by mated females, and that these unfertilized eggs produce normal larvae when eaten by the silkworms.

Unmated females of *Ptychomyia remota* at times deposit eggs, though these do not hatch. *Compsilura concinnata* may puncture the host caterpillar, as in normal larviposition, but neither eggs nor larvae are deposited. It appears to be the general habit to retain the eggs in the ovarioles until mating has taken place; if this does not occur, the eggs, in various stages of formation, then break down and are absorbed. Webber (1932) states, however, that the eggs of unmated females of *Carcelia laxifrons* Vill., *Phorocera agilis*, and others, do descend into the uterus and may be deposited eventually, whereas this never occurs in *Sturmia inconspicua*.

Several authors have pointed out that a wide fluctuation in relative numbers of the two sexes occurs at various times during the season. In some multibrooded species, the females predominate during the autumn. Allen (1926) concludes that a definite sexual segregation takes place in *Archytas analis* under certain field conditions. It is believed that the bulk of the females migrate to new areas shortly after mating, in case suitable hosts are not sufficiently abundant locally, leaving the males to mate with such females as may emerge later. The migratory or dispersion tendencies of the females appear to be lacking in the opposite sex. The same author (1925) mentions the occurrence of large gyrating swarms of *Winthemia quadripustulata*, consisting entirely of males, in localities lacking in host infestations and food sources.

EFFECT OF PARASITISM UPON THE HOST

The effect of tachinid parasitism upon adult hosts is variable and depends upon the age of the latter at the time of attack and the rapidity of larval development of the parasite itself. During the early larval stages, feeding is mainly upon the body fluids and the fat bodies, resulting

in the inhibition of development or the atrophy of the reproductive organs of the host, a condition of parasitic castration similar to that brought about by many Hymenoptera. In *C. cinerea*, which attacks *Popillia* beetles, parasitization normally takes place very soon after the emergence of the beetles, and this fact, combined with the lapse of only six days from egg deposition to death of the host, ensures that little or no oviposition by the latter will take place. Overwintering beetles of *Galerucella* which harbor the young larvae of *Erynnia nitida* are killed in the spring very soon after feeding begins, and no eggs are deposited. In *Eubiomyia calosomae*, which has several generations each year and attacks *Calosoma* beetles having an adult life of two or more years, the situation is somewhat different. The summer broods kill the host in 9 to 12 days, and overwintering parasitized beetles die within a few days after the beginning of activity in the spring. The effect upon the host population is much less than in the instances previously cited, because a large portion of the reproductive potential may already have been realized.

In orthopterous hosts, feeding by the parasite larva appears to be restricted quite largely to the blood, and it results primarily in a reduction of the fat bodies. A. W. Lopez states that mature larvae of *Ceracia aurifrons* Ald. have been taken from a number of locusts that had accomplished oviposition during the preceding 12 hours. Pantel (1898) has shown that the degeneration of the reproductive system of female Phasmidae as a result of parasitism by *Thrixion* is only temporary and that in some instances these females are again able to produce and deposit eggs after the parasite larvae have left their bodies. In the European earwig, which is most frequently attacked in the late nymphal instars, there is a partial atrophy of the reproductive organs, and death normally takes place before eggs can be laid.

Information is incomplete regarding the effect of parasitism upon Hemiptera. It is stated that the false chinch bug, *Nysius ericeae* Schill., is seldom able to deposit eggs when parasitized by *Hyalomya aldrichi*, whereas adult females of *Anasa tristis* DeG. containing larvae of *Trichopoda pennipes* (Worthley, 1924) oviposit, apparently without serious interruption, until the final larval stage of the parasite is attained. The parasitized individuals of the autumn brood, however, do not attain sexual maturity.

IMMATURE STAGES

The Egg.—There are four general types of egg produced by the Tachinidae, as follows:

1. *Macrotype.*—The eggs of this form have a very heavy and opaque dorsal chorion, with the ventral surface flat and the chorion thin and more or less transparent. They differ from other types principally in size, color, the stage of development of the

embryo at the time of deposition, and the manner in which hatching is accomplished, The general form is oblong, the anterior end being very nearly as wide as the posterior. and in lateral view they are markedly arched, at times approaching the hemispherical, with the ventral side flat or at times slightly concave. A few species of *Nemorilla* and *Gymnosoma* bear a distinct marginal flange at the juncture of the flat ventral surface with the lateral areas. In size, the eggs of the different species range from 0.4 to 0.9 mm. in length, with the width varying from one-third to two-thirds the length. The color is usually creamy- or glossy-white at the time of deposition, later changing to a gray or light brown. The micropylar area is usually dorsal and somewhat pigmented, though in *Gymnosoma* it is terminal or slightly ventral. In a few species, the surface of the chorion bears rather minute reticulate markings. Townsend describes the

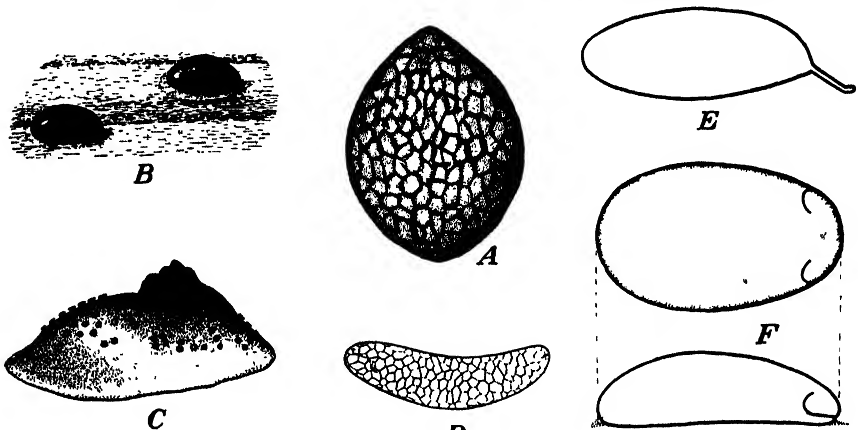


FIG. 207.—Eggs of the Tachinidae. *A*, the microtype egg of *Zenillia libatrix* Panz. (*from Dowden*, 1934); *B*, the same, of *Gonia capitata* deG. (*from Strickland*, 1923); *C*, the same, of *Racodineura antiqua* Fall. (*from Thompson*, 1920); *D*, the membranous egg of *Bonnetia comta* Fall. (*from Strickland*, 1923); *E*, the pedicellate egg of *Carcelia cheloniae* Rond. (*from Pantel*, 1910); *F*, the macrotype egg of *Winthemia* sp., dorsal and lateral views, showing the transverse line of fracture.

unusual egg of *Phasiopsis floridana* Tns. as asymmetrically long-ovate, the right side straight on the middle half and the left side evenly curved, and brown in color. It differs from those of other species, also, in revealing this coloration even before deposition.

The macrotype eggs are divided, on the basis of the manner of hatching, into two distinct groups termed "dehiscent" and "indehiscent" by Pantel. The latter form has no special provision for hatching, which is accomplished by cutting through the thin ventral shell directly into the host body. The eggs of *Centeter*, *Meigenia*, and *Trichopoda* are representative of this group. The dehiscent eggs have a distinct seam, or line of fracture, across the anterior margin, which curves backward and somewhat dorsad; at hatching, this seam is broken, and the lid is forced upward to permit the larva to emerge into the open. *Ptychomyia*, *Tricholyga*, and *Winthemia* (Fig. 209*F*) deposit eggs of this form. The macrotype eggs carry a quantity of mucilaginous material at the time of deposition, which fastens them securely to the body of the host. In some species, this material may be observed in regular loops or folds on the venter of the uterine egg.

2. *Microtype.*—This type of egg has many characters in common with the macrotype; as the name indicates, it is of minute size in relation to the body of the parent

female. The largest thus far recorded is that of *Chaetogaedia monticola*, which measures 0.44 by 0.25 mm. Thompson has given the measurements of a large number of eggs of this type, the great majority of which range from 0.02 to 0.2 mm. in length. Those of *Zenillia pullata* and *Pseudogonia cinarescens* Rond. are exceptionally minute, measuring 0.027 by 0.02 mm. and 0.08 by 0.056 mm., respectively. The majority are approximately two-thirds as wide as long, ranging to almost circular in *Phryno vetula* Meig. Townsend has calculated the volume of a considerable number of eggs of this family and finds that the large macrotype egg of *Gymnosoma*, which is 0.9 mm. long, is approximately two thousand times the volume of the microtype egg of *Z. pullata*. In general, microtype eggs are only about one-fiftieth as large by volume as macrotype eggs deposited by females of the same size.

The general form of the egg is ovate, with the anterior end narrower. In side view, the outline is somewhat semicircular, though often somewhat flattened; but in *Racodineura antiqua* (Fig. 207*C*) (Thompson, 1920*b*, '28) the dorsum is in the form of an asymmetrical cone, with the summit bearing an irregular group of strongly sclerotized elevations, which are surrounded by a number of small button-like structures, doubtfully considered to be respiratory papillae. With reference to *Otomasicera patella* Tns., the egg is described as limpet-like, with irregular concentric peripheral thickenings. Those of many genera of Exoristinae and of *Epidexia*, also, are very elongate, subelliptical, and pointed at both ends; they have submembranous chorion extensions and the dorsum is black, coarsely punctate, with reticulate markings and a median longitudinal suture.

The surface markings of the eggs of other species range from a very fine puncturation to a deep pitting or reticulate marking. The heavy chorion of the dorsum ranges in color from gray to brown and to the more frequent shining black, though Townsend lists several genera in which they are yellow or even white. In *Pexopsis aprica* Meig., there is a densely pigmented hemispherical process, of unknown significance, at the anterior end; the egg of *Sisyropa* sp., which has the reticulate surface, bears also an irregular, light-colored fringe around the margin, which is pierced with microscopic holes. On the ventral side, the chorion of the microtype egg is thin and transparent, though in *Gonia capitata* (Fig. 207*B*) the thickening and pigmentation are only reduced ventrally and are entirely lacking only on the median line. The micropyle is clearly recognizable in the eggs of many species and occurs at the narrower, anterior end. The embryo is enveloped by a tough vitelline membrane.

3. *Membranous.*—This type of egg is distinguished in general by its elongate form and thin transparent chorion. In size it is minute to large, ranging from 0.2 mm., about half the length of the largest microtype egg, to equal to the macrotype eggs from equal-sized females, and the length may be from three to six times the width. The ventral surface is not flattened and therefore does not permit of close attachment to the host or to foliage. Its form may range from long cylindrical, with both ends evenly rounded, to markedly arched or bowed, with the ventral line straight or concave and the anterior end appreciably narrowed. The micropyle is terminal and may be simple, of rosette form, or with various short processes, which are particularly noticeable on the ovarian eggs. The surface reticulations of the chorion, termed the "pneumatic apparatus" by Pantel, are often quite conspicuous, the lines being brownish in color. These reticulations may be complete, as in *Bonnetia comta* (Fig. 207*D*), limited to the middle portion of the egg, or of uneven distribution as in *Peleteria prompta* Meig.

These thin-shelled eggs hatch in the uterus of the female or almost immediately after deposition. The few species that deposit unincubated eggs of this type inject them into the body of the host.

4. *Pedicellate.*—In this group is placed the egg of *Carcelia* (Fig. 207*E*) which has a membranous chorion and bears a slender cylindrical pedicel, about one-fifth the length of the body, at the posterior end. This stalk is expanded at its distal end into an adhesive process, by means of which it is fastened to a hair or to the integument of the caterpillar body. Thus far, this modification is known to occur only in the above genus.

First-instar Larvae.—There are three general forms of first-instar larvae as follows:

1. *Tachiniform.*—The larvae included in this group are those which may be considered as normal for the family, and they have no marked modifications in form or structure to adapt them to a specialized mode of life. A number of larvae of this type have been described in detail by Thompson (1926). They include all those hatching from macrotype and pedicellate eggs, those which are injected into the body of the host, and finally, those from the membranous type of egg which, as fully incubated eggs or newly hatched larvae, are deposited upon the host body or in its

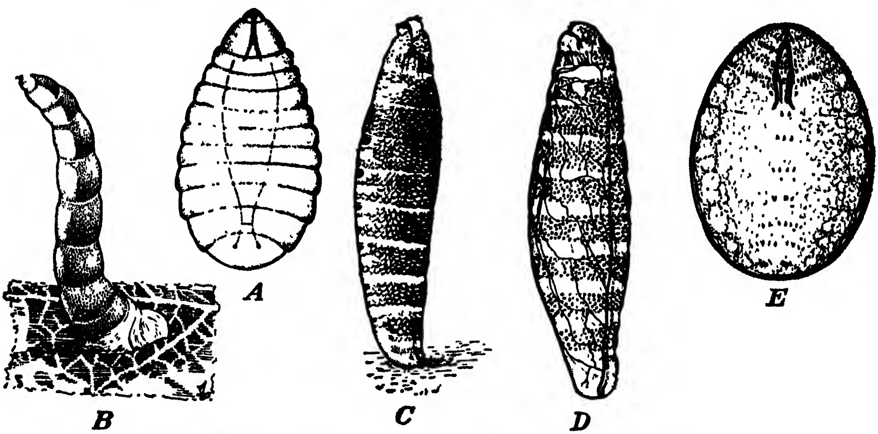


Fig. 208.—First-instar larvae of the Tachinidae. *A*, *Centeter cinerea* Ald.; *B*, *Eupeleteria magnicornis* Zett., showing the egg chorion serving as an attachment "cup" to the substratum; *C*, *Bonnetia comta* Fall. in the erect alert position; *D*, the same after feeding, showing the separation of the integumentary scales; *E*, *Parachaeta* sp., fully mature but still within the chorion. (*A*, *from Clausen et al.*, 1927; *B and E*, *from Townsend*, 1908; *C and D*, *from Strickland*, 1923.)

immediate vicinity. The latter are presumed to reach the host very quickly and consequently require no modification of the integument to protect them from desiccation and injury. The body is usually robust, with the cuticle colorless and transparent, and usually bears bands of rather minute spines on each segment, particularly at the margins, these bands being most frequently complete on the thoracic segments and predominantly ventral on the abdomen. A few species, such as *Centeter cinerea* (Fig. 208*A*) appear to lack the spine bands entirely. A definite adaptation for attachment to internal tissues or organs of the host is found in *Anetia*, *Compsilura*, *Paradexodes*, and some other genera. This consists of a set of three heavily sclerotized spiracular hooks at the caudal end of the body, each of the two dorsal ones being situated immediately above a spiracle and the third on the median line somewhat below them. The dorsal hooks are simple and sharply curved, with the points directed cephalad, whereas the median one is double- or triple-pointed and directed ventrad. These hooks are integumentary in origin and are not a part of the spiracular

structure itself, thus differing from the spiracular hooks in later instars of certain other species. In this group is also included the vesiculate larva of *Plagia trepida* which, if the adaptation were more highly developed and of more frequent occurrence, might constitute a separate type, as in the Hymenoptera.

2. *Microtype.*—These larvae, which are derived from microtype eggs that hatch within the digestive tract of the host, are of very small size and lack the various adaptations associated with a period of free life or with the necessity of penetrating a heavily chitinized host integument. The buccopharyngeal armature usually shows a reduction and simplification. Thompson (1924) has given detailed descriptions of the larvae of a large number of species, with keys for distinguishing them. The skin is thin and colorless and without any evidence of specialization except for the transverse rows of minute spines at both margins of the body segments, those on the abdomen usually being present only on the venter (Fig. 208*E*). In *Gonia capitata* and various other species, the first segment bears dorsally at its anterior margin a group of 10 to 12 strong hooks, which are heavily pigmented. In several species of *Gonia* described by Tothill, there are transverse rows of four hooks ventrally between the posterior segments, and the outer ones are connected by an internal chitinous rod. The larvae of *Racodineura antiqua*, *Brachychaeta spinigera* Rond., and *Pales pavida* Meig. lack the caudal spiracles, whereas in *Phryno vetula* they are present but very small and probably not functional. The spiracles are lacking also in *Exorista fimbriata* Meig., and the felt chamber is short, filiform, and almost invisible. The frequent absence of an open tracheal system in larvae of this type is correlated with their mode of life in this stage, during which they are usually embedded in some host organ. Except for its size and its association with the microtype egg, the microtype larva has few characters to distinguish it from the tachiniform larva.

3. *Planidium.*—The essential adaptive characters of the tachinid planidium are for the purpose of protection from injury and desiccation during a more or less protracted period of free life before the host is reached. They consist of a cuticular armature of closely set polygonal sclerotized plates, or imbricated scales, covering the dorsum and pleural areas, and in some species a large portion of the venter as well, of all body segments except the last, forming a carapace. Though most planidia have the armature in the form of scales or plates, yet in several species it is in the form of nodules or minute rounded protuberances surmounted by setae. Rows of spines occur ventrally upon the various segments. In *Fortisia foeda*, each body segment except the last bears many small oval plates, each of which terminates in a strongly sclerotized tooth (Thompson, 1915*c*). The extreme development of this type of larva in the family is found in *Gymnocheta alcedo* Lw. described by Thompson (1923*d*), in which each segment bears a single dorsal plate and a pair of pleural plates, and in species of *Ormia*, *Ormiophasia*, and *Euphasiopteryx* described by Townsend. The segments of the planidia of the latter genera are telescopic, and the plates occur in three series, the dorsal one being very wide and the others situated dorsolaterally and ventrolaterally. The venter is unsclerotized. *Ormiophasia* still further approaches the planidium type in that it possesses caudal cerci, a character found in the larvae of many Dexiinae.

The planidia are derived from eggs hatching in the uterus of the female or from membranous eggs deposited on the food plants of the host or in their general vicinity. They are variously colored, owing to the pigmentation of the plates, and may be grayish-white, brown, bluish-green, or black. As growth takes place, the plates become considerably separated, revealing the white body color. There is also an appreciable stretching of the thin intersegmental membranes, resulting in a distinctly banded appearance. This is noticeable even in the freshly deposited larvae of *A. analis*. The

species that retain the eggshell as an anchor to the substratum, and enveloping the caudal end of the body, have forwardly directed spines on the last one or two segments. Typical of this group are *Archytas analis*, *Bonnetia comta* (Fig. 208*C*, *D*), and *Ernestia ampelus*.

The first-instar larvae of *Ophirionopsis* and *Ophirion* are markedly different from other representatives of this group. They are described by Townsend (1936) as being somewhat caterpillar-like and very active; the former is stated to have eight pairs of "pseudolegs," which are half as long as the thickness of the body, and it has, in addition, three anal pseudopods. In *Ophirion*, the pseudolegs occur on the fourth to the tenth and on the twelfth and thirteenth segments.

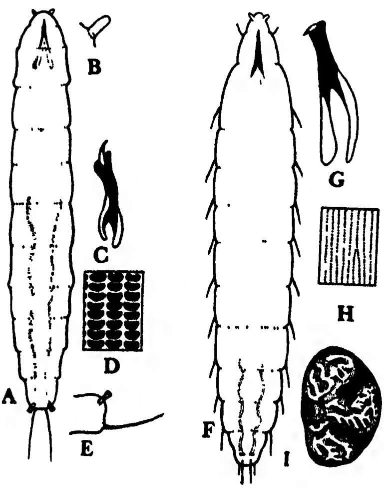


FIG. 209.—*A*, the first-instar larva of *Dexia ventralis* Ald.; *B*, antenna; *C*, the mouth hook; *D*, an enlarged portion of the integument showing the arrangement of plates; *E*, lateral view of the last abdominal segment. *F*, the first-instar larva of *Prosena sibirita* F.; with *G*, the mouth hook; and *H*, a portion of the integument. *I*, a posterior spiracle of the third-instar larva. (*From Clausen et al.*, 1927.)

The occurrence of light-colored planidia is exceptional and a number described as such are believed to represent larvae deposited prematurely or dissected from the uterus and mistakenly believed to be mature. All larvae of this type have open caudal spiracles.

The three first-instar larval forms described above are separated on the basis of adaptive characters, which are of independent development in widely separated genera and higher groups. The morphological characters of value in classification require too detailed treatment to be adequately summarized here, but in general they relate to various details of the head structure, the buccopharyngeal apparatus, the arrangement and form of the integumentary spines, the sensory organs, the caudal spiracles, etc. The principal studies upon the classification of these larvae have been by Thompson (1922; '23*b*, *c*; '24), who concludes that they present adequate characters for specific determination, though the groups set up on this basis are not always in accord with those based upon the taxonomy of the adults. He points out further that it is often difficult or impossible to distinguish between larvae of species which are quite distinct in the adult stage and, conversely, that it is at times possible to distinguish definitely between larvae of forms which, in the adult stage, are apparently identical morphologically (varieties of *Lydella stabulans* Meig.).

In practically all first-instar larvae thus far described, the number of abdominal segments recorded has been eight. There is a considerable range of variation in certain of the morphological characters that are not associated with a particular type of larva but that are used in the classification of the smaller groups. Some of these are discussed briefly herewith.

The buccopharyngeal apparatus consists, with very few exceptions, of a simple, unjointed structure, of which the three principal parts are the median tooth and the intermediate and basal regions, the latter of which may be only lightly sclerotized. The relative lengths of these three parts vary greatly. The outer, or dorsal, margin of the tooth may be smooth or bear a number of teeth. The lower wings of the basal

region are deflected somewhat ventrally, whereas the upper ones are usually considerably arched. There are frequently small lateral plates at the sides of the median tooth, and the small salivary-gland plate, often delicate and inconspicuous, lies beneath the intermediate region. The anterior lateral plates at each side of the median tooth can frequently be recognized, though they may be very lightly sclerotized. A distinctive form of the buccopharyngeal structure is found in *Bigonicheta setipennis*, in which the intermediate region is in the form of a straight elongate rod,

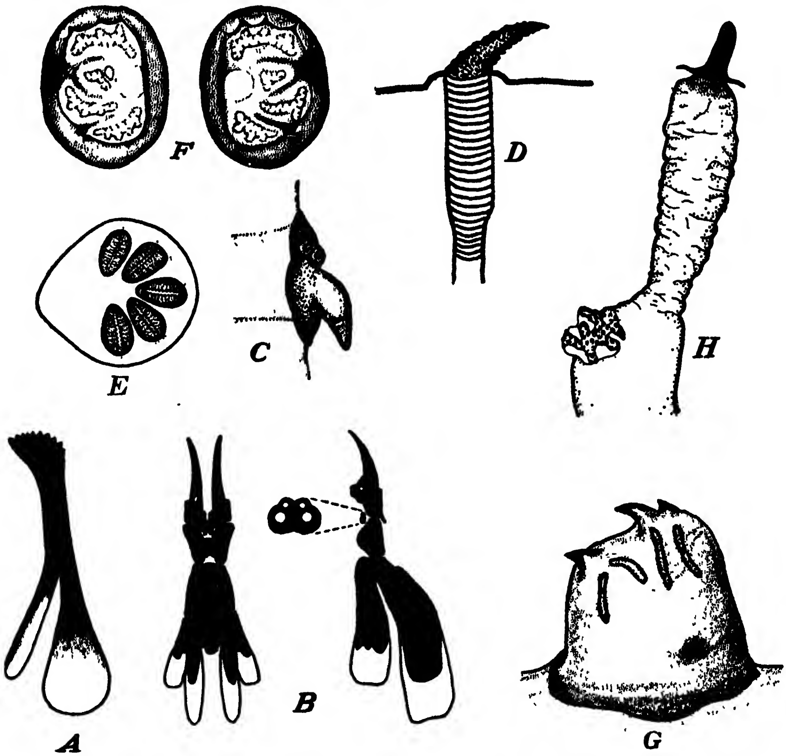


FIG. 210.—Details of larvae of the Tachinidae. *A*, the mouth hook of the first-instar larva of *Centeter cinerea* Ald. showing the rasping edge; *B*, mouth parts of third-instar larva of same; *C*, posterior spiracle of second-instar larva of same; *D*, posterior spiracle of second-instar larva of *Hamaxia incongrua* Tns.; *E* and *F*, anterior and posterior spiracles of the third-instar larva of *C. cinerea; G*, posterior spiracle of third-instar larva of *H. incongrua; H*, the pupal respiratory apparatus of *Anetia nigripes* Fall., showing the prothoracic cornicle and the internal spiracle. (*A–G, from Clausen et al.*, 1927; *H, from Dowden*, 1933.)

quadrangular in cross section and eight times longer than wide. The basal region is short and feebly developed.

The sensory organs of the head are usually not greatly developed and are most conspicuous in *Bigonicheta*. In addition to the usual maxillary sensoria, there is a pair of prominent clavate sensoria dorsally just in front of the antennae. The antennae are themselves remarkably developed, being cylindrical and about six times as long as wide, tapering abruptly to a point, and terminating in a hair-like distal portion about four times as long as the basal part. In addition to the sensory setae of the body segments, there are circular sensory organs on the venter of the various

segments. In some species, such as *Argentoepalpus signifer* Wlk. and others described and figured by Thompson, there are rod- or club-shaped sensoria on the thoracic and last abdominal segments. In many species, the antennae are small and somewhat conical in form, without a terminal hair.

The tracheal system of the first-instar larva, which is present in the very great majority of species, consists of two main longitudinal trunks, with relatively few branches; they are connected by a posterior commissure. The posterior spiracles usually consist of two papillae, each spiracle consequently being kidney-shaped in outline, though a few species have simple circular spiracles with only a single opening. In *Dexia ventralis* (Fig. 209*E*) and *Theresia claripalpis*, the spiracles are borne upon short cylindrical stalks; in *Billaea pectinata* Meig. (Tolg, 1910), the stalks equal one body segment in length, and they also bear three long setae at the distal end. The atrium, spiracular, or "felt" chamber may be only as long as wide (*Leschenaultia exul*) or range to 15 to 20 times the width (*Bigonicheta setipennis*). It has been mentioned that spiracles are lacking in a number of species of microtype larvae, and they are likewise missing in *Actia diffidens* and *Sturmia pelmatoprocta* B. & B. Anterior spiracles are quite uniformly absent in the first instar, though Landis states that they are present in *Paradexodes epilachnae.*

Second-instar Larvae.—The larvae of this instar show a much greater uniformity than do those of the preceding instar, as is to be expected in view of the occurrence of all species in the same environment, that is, within the body of the host. The factors of locomotion, desiccation, penetration, and mechanical injury are all absent; and consequently adaptations to meet these conditions are lacking. In all species, the integument is thin and transparent, the most conspicuous change in this respect being among the planidium-type larvae, which discard the heavy integumentary armature of plates, scales, etc., at the first molt.

In general, the cuticular armature of this instar consists of bands of setae, usually rather delicate, about the thoracic segments, on the venter of the abdominal segments, and in the form of a large patch on the last segment, often accompanied by a rather heavy band on the penultimate segment. These setae are often arranged in irregular and broken rows. In some species, the spines are much more numerous than in the preceding instar; in others, they are much less conspicuous. A number of species having heavily spined planidium-type larvae are, in this instar, virtually devoid of spines. In several species, rather conspicuous departures from the normal spine arrangement are known. The larva of *Gonia capitata* has patches of minute black spines on the dorsum of the first thoracic segment and on the venter of the second, which are so dense as to give the appearance of black plates. The spine patches on the venter of the last abdominal segment reach a maximum development in *Anetia hyphantriae* and are said to invaginate to serve as false feet, though the locomotory requirements of this instar are quite limited. The spines of the last two segments of the great majority of species are usually directed cephalad, and they serve to hold the larva more firmly in position in the respiratory funnel.

The larva of *Centeter cinerea* is distinguished from others of this instar by the possession of a pair of conspicuous anal lobes which may be homologous with those of the same instar of certain Conopidae.

The buccopharyngeal apparatus is more robust and highly developed in the second than in the first instar, and there is, of course, much variation in the form, relative size, and sclerotization of the different parts. In all species, the paired mandibular hooks are present, in contrast to the single median tooth of the first instar. A few species, such as *Zenillia libatrix*, *Bigonicheta setipennis*, and *G. capitata*, have no articulations, the entire structure apparently being fused into a single piece. The majority,

however, have one articulation, which is usually between the anterior and intermediate regions, though in some it is between the intermediate and basal regions. *Archytas analis*, *Bonnetia comta*, and *Siphona geniculata* have two articulations, separating the three principal parts of the structure.

The respiratory system of the second-instar larva is likewise much more highly developed than in the first instar, in consequence of the greater need for oxygen. The two longitudinal trunks are heavier, with a considerable number of branches, and both posterior and anterior commissures are present. In about half the species that have been studied, the anterior spiracles are said to be lacking, but in many instances they have probably been overlooked; for they are often very minute and situated intersegmentally in the pleural area between the first and second thoracic segments, and, in this position, any shrinkage or contraction of the body would tend to obscure them. Each anterior spiracle usually has two or three papillae, the number being increased to three to five in *Bigonicheta setipennis*, five to six in *S. geniculata*, and six to nine in *Lydella stabulans*. In *Ernestia ampelus*, however, they appear as simple circular openings, and those of *Billaea pectinata* are mere slits in the integument and are recognizable only in prepared sections.

The posterior spiracles of the majority of species are widely spaced and have two papillae, lobes, or spiracular slits, though *Actia diffidens* has only one and *Leschenaultia exul* and *Siphona geniculata* have three. An exceptional modification is present in the posterior spiracles of *Centeter* spp. (Fig. 210*C*) in the form of a large, ventrally directed, conical process immediately beneath the openings, which is believed to aid in perforating and maintaining connection with an air sac of the host. This process in *Hamaxia incongrua* (Fig. 210*D*) is more sharply pointed and directed dorsad. In *Anetia* and related forms, the stigmatic hooks, described for the first instar, persist in somewhat modified form. That they are functionless is improbable, in view of the development of a respiratory funnel during this stage. The spiracular chamber in most species is very short, often being broader than long. The only instance of complete lack of spiracles in the second-instar larva is that of *Fortisia foeda* cited by Thompson, though the internal tracheal system is present and the trunks are filled with air.

Third-instar Larvae.—The mature larva is usually somewhat crescentic in lateral view, with the venter concave and the abdominal region broadest. In some species, as *Chaetogaedia analis* v.d.W., the caudal segment is approximately the same width as those preceding it, whereas in others there is an appreciable tapering caudad. The segmentation is distinct, though frequently obscured by segmental folds. The larvae of *Zenillia roseanae* and *Actia diffidens* have distinct median pseudopodia ventrally between the abdominal segments. The anal opening occurs at a variable distance beneath the posterior spiracles, often near the anterior ventral margin of the last segment. The integumentary armature, consisting of spines and hairs, may be more or less extensive than on the preceding instar. The larvae of *Bonnetia comta*, *Bigonicheta setipennis*, *Racodineura antiqua*, *Dexia ventralis*, and *Prosena sibirita* are almost bare, whereas that of *Sturmia inconspicua* is almost completely covered with setae. More frequently, however, the thoracic segments and the last one or two abdominal segments bear complete bands of setae, whereas on the intervening segments they are largely ventral. The setae of the anterior segments are directed caudad and on the posterior segments usually cephalad. In *Centeter cinerea*, the central area of the last segment is covered with a patch of heavy black spines. The so-called spiracular hooks of *Zenillia* spp. persist in the form of clusters of three or four black spines, the bases of which are fused. These are apparently homologous with similar groups found in the same position on certain conopid larvae. The

sensory organs are often reduced in size and number as compared with those of the preceding instars. The four pairs of finger-like organs on the last segment persist in *Zenillia libatrix*.

The buccopharyngeal apparatus is more robust and highly developed than in the preceding instars. The majority of species now have distinct articulations separating the three principal regions. A considerable number of species, however, have only one articulation, which in some cases occurs between the anterior and intermediate regions and in others between the latter and the basal region. *Bigonicheta* is distinctive in having the entire structure in one solid piece. It is thus seen that the third-instar larvae of the family normally have two articulations, but frequently only one and rarely none; the second-instar larvae most frequently have one, but occasionally two or none; and the first-instar larvae usually have none, but very infrequently one or two. In no instance is a smaller number of articulations present than in the preceding instar of the same species. *B. setipennis* and a species given by Nielsen as *Ernestia connivens* Zett., but later stated to be *Plagia trepida* instead, have no articulations in any instar; *Zenillia* spp. have none in the first and second and one in the third instar; *Lydella stabulans* has none in the first and one in the following two instars; and *Leschenaultia* has none in the first two and two in the third instar. A number of species have none in the first and two in the last two instars. The greater number of species have none in the first, one in the second, and two in the third instar.

The anterior region is quite generally in the form of paired mandibles which are distinctly hooked. The hypopharyngeal and epipharyngeal sclerites are situated immediately beneath the juncture of the anterior and intermediate regions. Each of these bears clear areas which are believed to represent sensory organs. Those of the epipharyngeal sclerite particularly are variable in number and form and are considered to be of value in making specific determinations.

The respiratory system reaches its greatest development in the third-instar larva, as is to be expected from its greater size and the probable complete cessation of cutaneous respiration. It consists of a pair of heavy longitudinal trunks, anterior and posterior commissures, and anterior (occasionally absent) and posterior spiracles. In *Bonnetia comta*, each trunk is stated to have a diameter equal to one-fourth that of the body. According to Rennie and Sutherland (1920), *Siphona geniculata* lacks the anterior commissure.

The anterior spiracles are situated dorsolaterally at the posterior margin of the prothorax and may be in the form of a single circular opening as in *Winthemia quadripustulata;* a circular plate bearing radiating slits as in *Centeter* (Fig. 210*E*), *Hamaxia*, and *Bonnetia;* or, more commonly, a conical process bearing a number of papillae. These papillae may range in number from two to three in *Zenillia* spp. to 30 to 35 in *Billaea pectinata*. Occasionally, as in *Siphona* and *Racodineura*, the spiracle is fan-shaped, with the papillae in a row at the outer margin. In *Archytas analis* and *G. capitata*, the spiracular chamber itself is bifurcate, with an opening at the end of each short branch. In the former, the openings are elongate and curved. The spiracular chamber is usually two or three times longer than wide. The anterior spiracles are stated to be not recognizable if present in *Sturmia inconspicua* (Webber, 1932) and are lacking in *Leschenaultia exul*, though the stubs of the tracheal branches are present.

The posterior spiracles are usually large, somewhat circular in outline, with the inner margins more or less flattened, occasionally almost straight, and encircled by highly sclerotized, usually black, peritremes. In some instances, these spiracles are semicircular or even triangular in outline. The peritremes may be shallow, or

they may exceed the width of the spiracle, forming conical or subcylindrical bases. Occasionally, as in *Siphona* and *Ernestia rudis*, they are incomplete, being broken on the inner margin. In the great majority of species, the spiracles are situated above the transverse axis and occasionally are distinctly dorsal. Very seldom are they separated by a distance greater than the width of one spiracle, and frequently they are almost contiguous. The spiracular slits are usually straight or slightly curved and radiate outward from the spiracular scar, which itself is situated at or below the median transverse line and somewhat toward the inner margin. The number of these radiating slits is variable, most frequently being 3 or 4 but ranging up to 6 in *Eubiomyia calosomae* and about 10, variable and often branched, in *Bigonicheta*. In *Racodineura*, there are 30 short slits arranged side by side in the peripheral part of the respiratory area. Several species, such as *Gonia capitata*, show the smaller number of slits following the periphery rather than radiating from the vicinity of the scar. An occasional species has exceedingly long, serpentine slits, which at times are extensively branched. The three elongate slits of *G. capitata* and *Sturmia inconspicua* occur at the crests of pronounced ridges.

An unusual modification in form of the posterior spiracle is found in *H. incongrua* in which the face of the spiracle (Fig. 210*G*) is rounded and highly sclerotized, forming, with the peritreme, a broadly rounded cone surmounted at one side by three hook-like spines, which are directed laterad. In *Carcelia gnava*, the respiratory area is in three parts, with the openings small, irregular in form, without apparent order, and numbering about 30. The spiracle of *Steiniella callida* Meig. has 80 to 100 minute openings (Nielsen, 1909), and that of *Oedematocera dampfi* Ald. is rosette-shaped with the pores arranged in rows radiating from the center (Greene, 1927). The spiracles of *Fortisia foeda* are very large and bulbous and surmount short, broad stalks. The openings are small, irregularly placed, and very numerous. A remarkable form is figured by Lloyd for *Ginglymyia acrirostris*, in which the large spiracular stalks, which are oval in cross section, arise from a common base, pronouncedly dorsal in position, and each one terminates in an elongate-oval spiracle with a single elongate, curved opening at the center (Fig. 205*D*). At the outer margin of the spiracle are 30 leaf-like processes, of unknown function. These spiracles represent a wide departure from the normal tachinid form. In a number of species, several minute openings have been noted on the surface of the spiracle, which are stated to be those of the perispiracular glands. The spiracular chamber is relatively short in most species, seldom being longer than wide.

Puparia.—There is an exceedingly wide range of variation in form and general characters among the puparia of the Tachinidae. Those of a considerable number of species have been described in connection with biological studies of particular species, but the most detailed account yet available is that by Greene (1922), in which the puparia of 100 species of muscoid flies, a large portion of which are of this family, are described and figured. The author concludes that the puparial characters are adequate for specific determination.

The general form of the puparium is subelliptical and slightly widest in the mid-abdominal area, with both ends smoothly rounded. In a few species, such as *Hamaxia incongrua*, *Cryptomeigenia aurifacies* Walt., and *Viviania georgiae* B. & B., the abdominal region is much larger than the anterior, though occasionally it is somewhat narrower. The posterior end is at times markedly truncate, as in *Sturmia cubaecola* and *Chaetogaedia analis* v.d.W., whereas in others the caudal segments may be progressively narrower, giving a distinctly pointed appearance. Usually, the longitudinal axis is straight, though in *Eutrixa exile* Coq. there is a marked upward curve of the anterior region. The segmentation is usually indistinct and is indicated by

faint lines or by a variation in the pubescence; yet in *Exorista confinis* Fall. the intersegmental constrictions are very distinct on the entire periphery, and in several species they are pronounced on the dorsum. In *Pyraustomyia penitalis* Coq. and others, the last abdominal segment is much reduced, forming a tubercle surmounted by the spiracles. The anal opening is represented by a distinct groove at a varying distance below the spiracles, frequently occurring almost at the anterior ventral margin of the last segment.

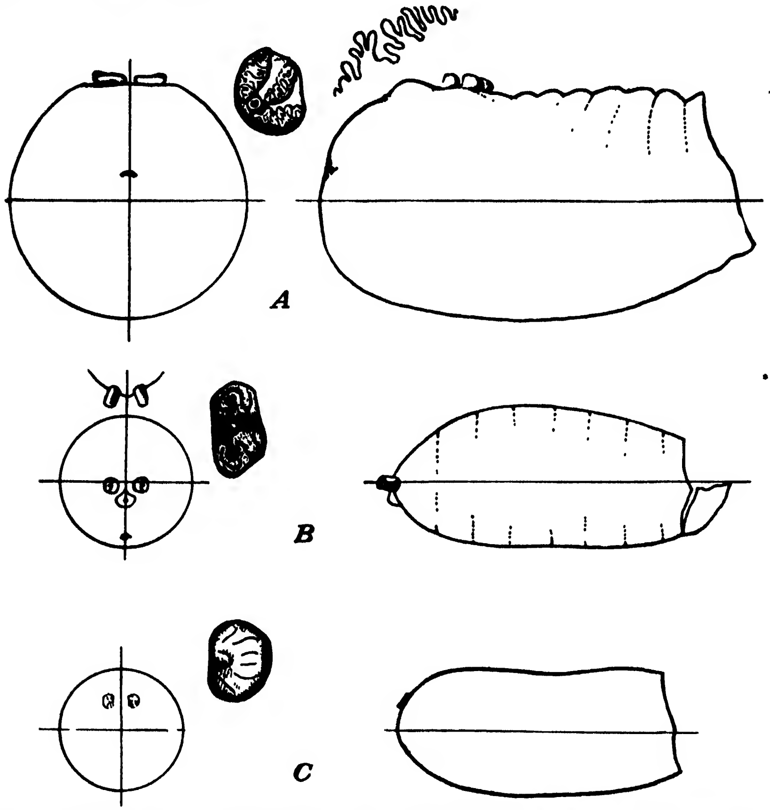


FIG. 211.—Puparia of the Tachinidae, with details. *A*, *Latreillimyia bifasciata* F.; *B*, *Exorista lobeliae* Coq.; *C*, *Cryptomeigenia theutis* Wlk. (*From Greene*, 1921.)

The color of the puparia of any given species is quite variable and usually deepens appreciably with age. In general, it ranges from the darker shades of red and brown to black and may be dull or have a silken luster. The puparia of a considerable number of species are yellowish-red, and that of *Alophora pulverea* Coq. is pale-yellow. The outer surface of the puparium bears the armature of the third-instar larva and may consequently be hairy, bare and smooth, or roughened by striations or rugosities.

The anterior and posterior spiracles are, of course, those of the third-instar larva; and although they are still recognizable as such, yet they show appreciable changes. The posterior ones are generally situated slightly above the transverse axis of the body; but they are definitely dorsal in *Latreillimyia bifasciata* (Fig. 211*A*), though they are below the axis in a considerable number of species and conspicuously so in

Tachinophyto floridensis Tns. They may be only slightly raised above the surface of the puparium or borne upon pronounced tubercles, as in *Anachaetopsis tortricis* Coq. The spiracular slits correspond in form to those of the mature larvae. The outstanding variation in spiracle form and position is found in *Ginglymyia acrirostris*, which bears them on large and heavy individual stalks markedly dorsad in position. The puparium of *Thrixion halidayanum* is distinguished by the occurrence of the

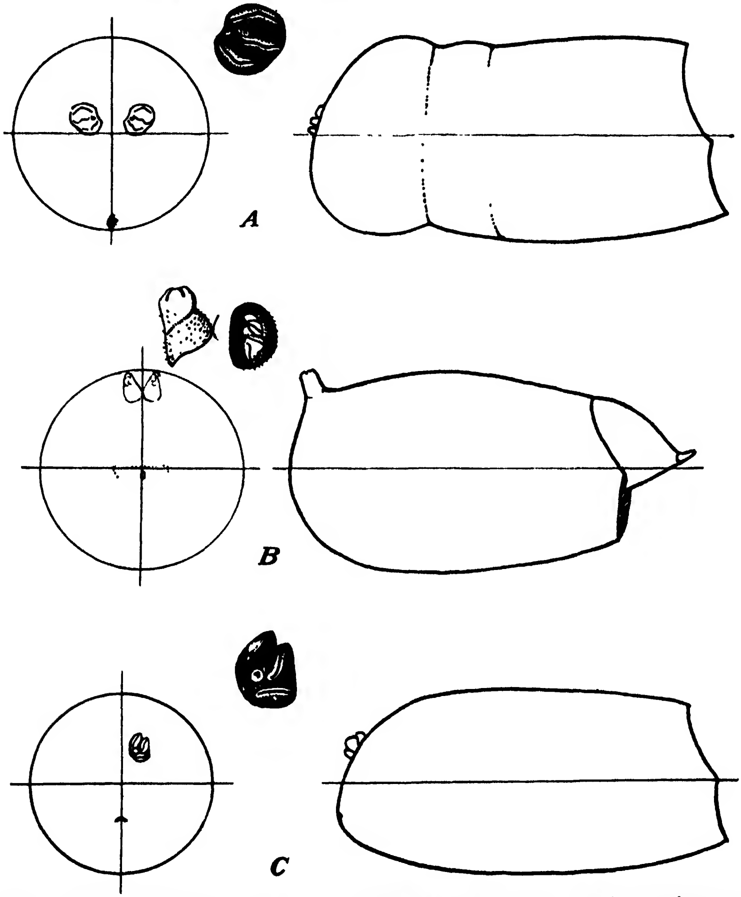


FIG. 212.—Puparia of the Tachinidae. *A*, *Archytas hystrix* F.; *B*, *Plagia americana* v.d.W.; *C*, *Gonia capitata* deG. (*From Greene*, 1921.)

spiracles upon a common stalk, which is large and cylindrical and projects from the rounded posterior end.

The external prothoracic cornicles are lacking in the majority of species, but in those which bear them they appear as conical or subcylindrical projections through the puparial wall dorsolaterally near the posterior margin of the fourth segment. The papillae usually number 6 to 20, though in *Leschenaultia exul* they exceed 100, distributed irregularly over the distal half of the cornicle. In *Actia diffidens* there is only a single terminal opening. In *Siphona geniculata*, the perforations through the puparial wall may be detected, though the cornicles do not protrude.

The internal prothoracic spiracles of the pupa (Fig. 210*H*), situated at the base of the prothoracic cornicles and beneath the puparial wall, are present in all species. They are circular in outline and nearly flat and usually bear the minute papillae in double rows radiating from the center. These rows are irregular and sometimes branching and number five or six in *Zenillia libatrix*. The total number of papillae in the great majority of species is 100 to 200.

There are two lines of cleavage which separate the two halves of the puparial cap from each other and from the remainder of the puparial wall, and both these halves are broken away at the time of emergence of the adult fly. The horizontal line of cleavage, separating the two halves, extends across the front and posteriorly at each side to a point in the anterior portion of the fourth segment. The vertical line of cleavage passes completely around the puparium and through these points and is in front of the prothoracic cornicles of the pupa, if they are present.

LEPIDOPTERA

The representatives of this order provide an excellent illustration of the development of the entomophagous habit in a large number of families that are normally phytophagous. Brues (1936) has given a general summary of the information available on the predaceous and parasitic groups of the order and discusses the manner in which the change from plant to animal food has come about. Balduf (1931) has reviewed the information relating to the predatory and parasitic species and more recently (1938) has presented a very interesting discussion of the origin and rise of the entomophagous habit among the larvae of the order. The order is, of course, essentially phytophagous, and the present entomophagous forms are believed to be derived principally from cortex- and lichen-feeding ancestors. He considers that the habit is now of four general types—cannibalism, occasional predatism, habitual predatism, and parasitism. Cannibalism represents an occasional diversion from the normal plant-feeding habit and results primarily from hunger or thirst. Occasional predatism is divided into two subtypes; the first is found among caterpillars of plant-feeding habit, which at times attack insects beyond their own species, and the second among the scavengers, which at times prey upon other species occupying the same habitat. Habitual predators are likewise divided into two distinct groups; the first is represented by a number of families having larvae that feed upon Homoptera, and the second, comprising a relatively few species of Lycaenidae, is distinguished by at first being phytophagous but then changing to the predaceous habit in the later larval stages.

Among the butterflies, the predaceous habit is found only in the family Lycaenidae, whereas among the moths it occurs in a considerable number of families and varies in the extent of its development from occasional or chance predatism to the obligatory role. The entomophagous habit reaches its highest development in the Epipyropidae, some of which are obligate external parasites, and the individuals of all species are limited to a single host during larval development. Instances of true parasitism by members of other families are exceedingly rare.

It is particularly noteworthy that the great majority of the hosts of the predaceous Lepidoptera are of the homopterous families Aphididae, Coccidae, Cicadellidae, and Fulgoridae. Limitation to these groups is considered by Balduf to be a result of their greater availability as compared with other plant-feeding insects. They occur generally in all

sections and upon a wide variety of plants, are usually present in abundance, and are soft-bodied and of small size.

LYCAENIDAE

In many ways this is the most interesting of the lepidopterous families, not only because of the large number of species that are of predaceous habit but because of the close and varied relationships that have developed between them and their hosts and associated insects. The subfamilies Gerydinae and Liphyrinae are exclusively predaceous, whereas some representatives of the Lycaeninae have this habit only in the last larval stage. Extended accounts of the biology and habits of the predaceous butterflies have been presented by Farquharson (1922) and Clark (1926), and more recently Balduf (1938) has reviewed the interrelations known to occur between members of this family and the ants and Homoptera with which they are associated. He divides the species into six classes on the basis of their food habits and of their relations with ants. The latter are of particular interest. In many cases, the caterpillars and ants are really competitors for a common food supply, and the secretions of the special glands of the former are, in reality, a bribe to induce the ants to tolerate their presence.

The predaceous members of the family prey most commonly upon Aphididae and Coccidae (particularly *Pseudococcus*), but also upon Cicadellidae and Membracidae and the immature stages of Formicidae. *Feniseca tarquinius* F., a North American species, was the first of the family found to have the predaceous habit. It feeds in all its larval stages solely upon aphids, such as *Schizoneura*, *Prociphilus*, and *Pemphigus*. Edwards (1886) and Clark have given detailed accounts of their observations upon it. The eggs are laid singly among the aphid colonies, always on the underside of the twig. The newly hatched larva spins a loose web over its body, beneath the aphids, that is presumably for protective purposes. Feeding takes place from beneath. The long hairs of the dorsum of the body entangle a considerable quantity of waxy material, giving the larva a woolly appearance. These larvae appear to be quite immune to attack by ants tending the aphid colonies. They have a variable color pattern, due, in part at least, to the species of aphid that is attacked. There are four larval instars and pupation probably takes place in the trash beneath the tree. The egg, larval, and pupal stages cover 3 to 4, 10, and 8 to 11 days, respectively. There are three to five generations each year, and the winter is passed in the pupal stage.

The various species of *Spalgis* are most frequently found as predators of mealybugs, though they attack aphids, also. *S. epius* Westw. (Aitken, 1894) of tropical Asia deposits its eggs among the masses of mealybugs.

The flattened, greenish-colored larva bears a fringe of bristles about the sides and front of the body, and this is utilized in shoveling the waxy covering of the host onto its back. This covering gives it a resemblance to the host individuals, though the older caterpillars are considerably larger and have a marked resemblance to syrphid larvae. Only the younger stages of the host are attacked. Larvae have been observed even within ant nests, feeding upon mealybugs which were being harbored therein.

The pupae of *Feniseca* and *Spalgis* are of peculiar form and have a color pattern that is said to give them a striking resemblance to a monkey's face.

The larvae of the known species of *Lachnocnema* are associated with Cicadellidae, upon which they are predaceous; but the incomplete information available indicates that they also feed to a certain extent upon the secretions of the leaf hoppers, and they may possibly be fed by the ants.

The genus *Lycaena* is of particular interest because of the interrelations that have developed between its members and their ant hosts. Oviposition apparently takes place mainly upon food plants beneath which ant colonies are located. The young larvae are exclusively plant feeders, but in the last stage they refuse such food and find their way or are carried into the ant nest, where they feed upon the ant larvae and pupae. A pronounced cannibalistic tendency is shown by the larvae during the plant-feeding period, which is entirely absent after entry into the ant nest. In these species, the last-instar larvae are equipped with a special gland on the dorsum of the tenth segment, from which is secreted a clear, liquid substance much sought after by the ants. Thus the ants are bribed, as it were, into tolerating or even cultivating the presence of these enemies of their own brood.

Clark has summarized the observations of a number of authors on the habits of *L. arion*. The third-instar larvae do not evacuate the hindgut until immediately before pupation, a departure from normal that recalls the habit of the great majority of parasitic insects and of some predators in other orders. Examination of the excrement revealed many dermal hairs and mandibles of *Myrmica*, thus definitely establishing the predaceous habit. Pupation takes place the following spring *in situ* in the ant nest or in the soil near by. The first three larval instars feed only upon thyme, and it is only in the fourth stage that the larvae enter the nests of *Myrmica*. The life cycle covers one year of which 10 months represents the larval period, and all of this, with the exception of the first two weeks, is passed in the ant nest.

In the subfamily Gerydinae, the larvae feed solely upon other insects, particularly the Homoptera. *Gerydus chinensis* Feld. is found most

commonly among aphids, and the larvae are stated to consume about 20 individuals per day (Kershaw, 1905). The victims are often seized with the forelegs and held in the air while being eaten. The eggs are deposited directly among the aphids and the ants attending them, and the female at times even thrusts them aside with her ovipositor in order to accomplish oviposition. *Megalopalpus zymna* D. & H. (Lamborn, 1914) differs from the above in that it is intimately associated with ants of the genus *Pheidole* during the developmental period. The food of the larvae is, however, the nymphs of Cicadellidae and Membracidae enclosed within the ant shelters. The female butterfly deposits her eggs singly in the neighborhood of such shelters as contain the proper hosts. Occasionally, she may place them directly upon an egg mass or upon the host body. The act of attacking a host reveals an interesting adaptation whereby capture is accomplished readily. The larva approaches the host with its legs raised and vibrating and causes them to caress the wings of the latter, thus simulating the ministrations given by the ants with their antennae. Finally, the head attains a position directly over the body, whereupon the victim is seized between the legs and feeding then takes place at a point just behind the head. As this progresses, the body of the prey may be raised into the air. Both nymphs and adults are attacked, though the former much more extensively. The *Megalopalpus* larva is protected by a hard skin, which is studded with tubercles surmounted by coarse hairs. The ants derive no benefit from their presence in the shelter and consequently are not attentive to them. The adult butterflies have the very unusual habit of feeding also upon the body secretions of the same hosts, rather than upon nectar and honeydew. They probe the body with the proboscis and apparently derive some food substance from the secretions. They have also been noted to do likewise upon the plant surface on which the hosts rest.

Several species of Liphyrinae have been studied in considerable detail, and they reveal numerous modifications in habit incident to the predaceous mode of life. Dodd (1902) has given an excellent account of *Liphyra brassolis* F., the caterpillars of which feed upon the larvae of the green tree ant, *Oecophylla smaragdina* F., in Australia. The eggs are usually deposited in pairs upon the branches or trunks of trees containing ant colonies, and the young larvae make their way into the nest. Apparently they also move from nest to nest during the feeding period. Pupation takes place in the host nest. The last larval skin is not discarded but remains in changed form as an outer covering for the pupa. The adult moths are covered with an abundance of loose scales apparently held together by an oily material. This covering is stated to serve as a protection from the very aggressive host ants, particularly at the time of emergence of the moth.

Euliphyra mirifica Holl., which is found in the nests of *Oecophylla* in Africa, apparently is not predaceous; instead, the larvae are fed by the ants. The species of the genus *Aslauga* that have been observed in the field are predaceous upon Coccidae, particularly the soft scales and mealybugs. The larvae have a hard integument, covered with tubercles, which provides protection from ants attendant upon the hosts. According to Balduf, this genus has arisen from lichen-feeding ancestors, and the change to the coccid-feeding habit has come about gradually; first, coccids were intermingled among the lichens and consumed indiscriminately, and then, during times when the growth of lichens was prevented periodically by adverse conditions, the larvae were confronted with a choice between starvation and subsisting upon the Coccidae alone. The change in habit was a consequence of a change in the available food supply.

EPIPYROPIDAE

All the known members of this family of minute moths are parasitic (in the zoological rather than the more restricted entomological sense) in habit and attack principally Homoptera of the family Fulgoridae, though an occasional species is recorded upon Cicadellidae and one species occurs upon Cicadidae in Japan. The family is particularly well-represented in the Australian fauna, and Perkins (1905*b*) observed the cocoons by the millions on the foliage of *Terminalia* in Queensland, giving the general appearance of a heavy infestation of *Pulvinaria*. A number of species are recorded from India. Westwood (1876) observed larvae of *Epipyrops anomala* Westw., upon the bodies of *Fulgora candelaria* L. and came to the conclusion that they were feeding principally upon the cottony secretion which covers the body of this insect. Subramaniam (1922) noted that the larger larvae of *E. fuliginosa* Tams scraped the side of the host body with their mandibles, possibly to feed upon the secretions. No apparent injury was inflicted, and the leaf hoppers appeared to be healthy long after the larvae had left them. Later investigations by various workers have indicated, however, that the larvae of some species of the family, at least, are definitely parasitic and that the scraping and removal of wax are incidental to the efforts of the larvae to penetrate the body wall of the host. One of the principal arguments supporting the parasitic relationship is the fact that the hosts of some species have no wax covering over the body. In these cases, it has been asserted that feeding may take place upon the honeydew, which is given off in copious quantities. T. B. Fletcher has called attention to the very long, slender mandibles of the larvae, which are more fitted for penetrating the body wall than for use in feeding upon the external secretions.

The most complete account of the habits of a member of the family is that by Krishnamurti (1933) for *E. eurybrachydis* Fletcher, which develops as a solitary or gregarious external parasite on the adult females of the fulgorid, *Eurybrachys tomentosa* F., in India. None has been observed upon nymphs or male adults. The eggs are dirty golden-yellow in color, oval in form, and measure 0.5 mm. in length. They are deposited in series of irregular rows upon the foliage of the food plant of the host.

Each female produces a total of 400 to 500 eggs. Incubation is complete in six to eight days, and the young larvae wander about on the foliage in search of hosts. They are often observed in an erect position, clinging to the margins of leaves by the prolegs, and waving back and forth as if awaiting a host. There are five larval instars, the first of which is 1.25 mm. in length, with 13 body segments which decrease in width caudad. The legs are short, five-jointed, and terminate in a curved claw. The mandibles are bidentate.

The younger stages are found at various points on the host body. The older individuals are usually beneath the wings, at one side of the median line, and they lie with the head directed caudad. The presence of one of these parasitic larvae upon the fulgorid body is always indicated by the elevated position of the wing on one side. The mandibles are embedded in an aperture in the integument of the abdomen. An examination of the contents of the digestive tract failed to reveal the presence of any waxy material. The effect of parasitism upon the host is relatively slight, for the amount of body fluids abstracted is comparatively small in relation to the size of the host and is evidenced only by a certain degree of weakness. The duration of adult life is not appreciably shortened, nor is egg production reduced. The larval feeding period of the parasite covers 42 to 45 days, and adult life 8 to 10 days.

When feeding is completed, the mature larva, which is now 7 to 8 mm. in length, leaves the host and spins its oval, milky-white cocoon on the underside of a twig. The pupa emerges partly from the cocoon just prior to the issuance of the adult moth. Oviposition begins 24 to 36 hours after emergence from the cocoon.

Less extended observations have been made upon the habits of several other species, principal among which are *Agamopsyche trenodes* Perk. (Perkins, 1905*b*) and *Epipyrops doddi* Roths. (Dodd, in Rothschild, 1906).

A considerable variation apparently exists with regard to the sex and stage of the host attacked. *A. trenodes* attacks the adults of both sexes of various Cicadellidae. Perkins mentions, however, that other species of the family have been noted upon nymphs as well as adults.

The majority of investigators who have studied species of this family consider that feeding of the larvae produces little or no effect upon the host. In *A. trenodes*, however, the parasitized leaf hoppers showed a distinctive collapse of the dorsum of the abdomen, and Koebele's observations indicate that death takes place the day following the quitting of the host by the mature larva. This is also said to be true in the case of *E. barberiana* Dyar, which develops upon *Ormenis pruinosa* Say in North America.

The position of the *Epipyrops* larvae upon the host body is quite uniform, being on the dorsum of the anterior portion of the abdomen beneath the wing, and with the head directed caudad. In *E. fuliginosa*, the tip of the abdomen is said to be attached to the side of the thorax. *Epipomponia nawai* Dyar, which attacks adult Cicadidae in Japan, is small in comparison with the host and is found on the venter of the thorax or on the venter or dorsum of the abdomen. The fact that the larvae maintain a fixed position upon the body of the host further supports the belief in a parasitic relationship.

Aside from Krishnamurti's observations upon oviposition by *Epipyrops eurybrachydis*, Perkins mentions that the disk-like eggs of *Agamopsyche* are deposited in large batches upon dead grass and leaves in the same environment in which the cocoons are found. There is little reason to doubt, however, that the eggs of other species also are deposited in clusters upon foliage or twigs in the general vicinity of feeding hosts and that the first-instar larvae must either search for their hosts or wait until they come within reach.

The life-history studies that have been conducted indicate a relatively short cycle, from egg to adult, of approximately one month, of which about half comprises the larval feeding period. The cocoon stage of *E. doddi* covers 13 to 17 days, and that of *E. anomala* 9 days. Little is known regarding the sex ratio or parthenogenesis. Perkins states that *Agamopsyche* is unisexual and that no males have been observed. Fertile eggs were produced by virgin females under cage conditions. Males have been described, however, in species of several other genera.

The first-instar larvae of this family are of particular interest because of the adaptive characters developed as a consequence of their unusual mode of life. The very slender, tapering body, with the comparatively strong legs, is obviously an adaptation for a free-living period during which search for the host takes place. This larva shows a tendency toward assumption of the planidium form found in other orders, which has been developed to meet quite similar requirements, and it is able to stand erect by the use of the anal prolegs, a habit quite general among larvae of this type in many families and several orders.

Following the first molt, the legs became greatly reduced and the later instars are virtually sessile. The head and mouth parts of all instars are markedly modified as a result of the manner of feeding that has been developed. The body becomes either oval or almost circular in outline, and a distinctly "coccus-like" form is assumed. This is accentuated by the presence of an extensive waxy covering over the body. In the case of *Agamopsyche*, it was noted that the larger larvae were able to suspend themselves from the host body by a silken thread.

The cocoons are white in color, with a mealy surface appearance, and there is considerable variation in form and surface ornamentation. Usually there are numerous longitudinal ridges. The cocoon of an undetermined species observed by Koebele in Australia is rosette-like and nearly circular and has several vertical lamellae arranged concentrically about the more solid center. In all species, so far as known, the empty pupal case is found partly extruded from the cocoon.

PSYCHIDAE

The bagworms are well-known as plant pests, but very few records are available regarding their attack upon other insects. Plank and Cressman (1934) observed extensive feeding by the larvae of *Platoeceticus gloverii* Pack. upon the camphor scale, *Pseudaonidia duplex* Ckll., in Louisiana. This species is normally a plant feeder; yet in 1932 it was estimated that well over 90 per cent of the scales in a heavy infestation on camphor were destroyed by it. Feeding of this type takes place largely during the winter months, and very little is noted during the summer. Larvae feeding upon scale usually remove the dorsal coverings completely and incorporate them into the larval case.

OINOPHILIDAE

An occasional species is recorded as having developed the predatory habit, though apparently only incidentally. *Ereunetis minuscula* Wesm. is said to be predaceous upon the cottony-cushion scale and other scale insects in Puerto Rico. It is, however, primarily a plant scavenger.

CYCLOTORNIDAE

One of the most striking adaptations in habit to meet food requirements is exhibited by the Australian *Cyclotorna monocentra* Meyr. (Dodd, 1912) and others of that genus. The young larvae are parasitic or predaceous upon Cicadellidae, whereas the later stages subsist entirely upon the body fluids of ant larvae. This obligatory change of food source at an intermediate point in the larval period is most unusual and would seem to subject the species to a considerable hazard. Further,

the larvae are dependent upon the services of the ants themselves in order to gain access to the nest.

The female moth deposits her eggs in large numbers upon the twigs in the vicinity of colonies of leaf hoppers. Upon hatching, the young larvae move about until a victim is encountered, whereupon they attach themselves and begin to feed. They move about somewhat over the body of the host and are later found almost exclusively upon the abdomen. On hosts sufficiently developed to possess wing pads, the feeding point is usually beneath one of these, which is consequently forced out of its normal position. From one to eight larvae may be found on a single hopper. A web of silk, which is extended at one side to form a delicate wall, is spun beneath the body. It is probable that a portion of the hosts that are attacked die without attaining the adult stage, though the exact effect of attack has not been determined. The larvae occasionally move from one host to another, and consequently they are more properly classed as predators, though far advanced toward obligate parasitism.

Before the completion of the first stage, the larvae leave their leaf-hopper hosts and construct a light, flat, oval "cocoon" within which the first molt takes place. The second-instar larva emerges from this cocoon three days later and moves away for a short distance, after which it assumes a peculiar attitude, with both ends of the body raised so that they nearly meet over the dorsum. When these larvae are encountered by mound ants, *Iriodomyrmex purpureus* Smith, they are immediately seized and carried into the nest. Here they feed upon the body fluids of the ant larvae and at the same time provide food for the ants through their secretions. When growth is complete, the larvae leave the ant nest and ascend a near-by tree, where the cocoons are spun in crevices in the bark, etc. At emergence, the pupal skin remains partly extruded from the mouth of the cocoon. The pupal stage covers 19 to 20 days.

The eggs are minute in size and oblong in form and bear pronounced longitudinal striations. The first-instar larvae are oval in outline and quite flat, with a median longitudinal ridge, and are at first dull-yellowish in color but later change to pink. The number of molts has not been definitely determined, but no appreciable differences can be found between the early second instar and the mature form. They have a marked resemblance in form to wood lice. The body of the second-instar larva is very flat and is oval in outline, with a distinct median dorsal ridge, and each segment bears at its lateral margin a fleshy pointed process. Those on the last segment are produced into a pair of tail-like processes about equal to the body in length. The initial color is orange-red dorsally and white ventrally, which changes to pink and greenish-blue or blue. This coloration is due to the body contents being visible

through the transparent integument. The larvae of *C. experta* Meyr. may be distinguished by the absence of these lateral and caudal processes.

BLASTOBASIDAE

The predaceous habit in this family is largely restricted to the genus *Holcocera,* which is generally associated with lecaniine Coccidae. Some species are thought to be mainly scavengers rather than feeders upon living scales. The well-known *H. pulverea* Meyr., which attacks the lac insect in India, causes serious losses to the industry, not only through the destruction of living scale upon the trees but through the infestation of stored lac. At times, the damage in the fields amounts to 25 to 30 per cent. According to Glover (1933), the eggs are deposited singly upon either adult female scales, empty male cocoons, or twigs having a heavy growth of sooty-mold fungus as a result of the scale infestation. The young larvae feed upon the body contents of the scale as well as upon the waxy covering. They progress from one scale to another, building a silken tunnel or web through the mass. A maximum of 45 adult female scales may be killed, and the wax covering partly destroyed, by each larva during its feeding period. There are five generations each year, and the winter is passed mainly in the egg stage. The eggs appear to be very susceptible to climatic changes; for there is a high winter mortality, and, in addition, the great majority of those deposited during June are killed by the high temperatures that prevail at that time.

H. iceryaella Riley of western North America, which attacks *Lecanium persicae* F. and other lecaniine and diaspine Coccidae, is of similar habit. There is still some question as to whether feeding is predominantly upon living or dead scales. Basinger (1924) has discovered that the larvae of this species have developed the habit of feeding upon citrus fruit in California. They make holes or channels into orange fruits that are somewhat similar to those made by *Tortrix citrana* Fern. *Blastobasis transcripta* Meyr. is an enemy of *Ripersia* in India. *Zenodochium coccivorella* Ch. is recorded by Comstock as an internal parasite of the gall-like females of *Kermes* in Florida, but it is more probably a specialized predator upon the eggs in the egg chamber, and restricted to the product of a single female.

HELIODINIDAE

In Australia and India, a number of species of the genus *Stathmopoda* are recorded as insect feeders, principally upon Coccidae. *S. theoris* Meyr., though normally a vegetable feeder, is a serious enemy of the lac insect, and several species of *Oedematopoda* also attack this host. *S. arachnophthora* Turn. feeds upon spider eggs in Queensland.

An aberrant species, *Euclemensia bassettella* Clemens, is recorded by Hollinger and Parks (1919) as a very common predator upon *Kermes galliformis* Riley in Texas, and it has also been reared from several other members of the genus. Feeding apparently takes place upon the adult female scales as well as upon the large mass of eggs beneath them. Prior to pupation, the mature larva cuts a circular or oval hole in the dorsum of the scale body and closes the opening with a mesh of silk. A single generation is produced each year, corresponding to the cycle of the host, and the adults appear in midsummer.

OLETHREUTIDAE

Bevis (1923) gives a short account of the habits of *Coccathera spissana* Zell. as an enemy of *Ceroplastes egbarium* Ckll. in South Africa. Although the exact relationship was not definitely determined, yet it appears most probable that the larvae are predaceous upon the eggs in the chamber beneath the female body. A large proportion of the scales examined showed one to three emergence holes in the dorsum. The mature larva measures 4.5 mm. in length. The empty pupal case remains partly extended from the emergence hole.

TORTRICIDAE

Only an occasional species is known to depart from the normal plant feeding habit and to attack other insects. *Tortrix callopista* Dur. is recorded by Lamborn (1914) as being predaceous upon *Stictococcus* in West Africa. The larvae tunnel among the scales and eat away the body contents from beneath.

PHYCITIDAE

Several members of this family feed exclusively upon other insects, more particularly those of the same order and the Homoptera. *Phycita dentilinella* Hamp. is predaceous upon the pupae of several Lepidoptera in India. Ayyar (1929) states that during some seasons it is found in a considerable proportion of the cocoons of the "nettle grub," *Parasa lepida* Cram. Considering the hard, shell-like nature of the cocoon of this moth, it appears probable that the young *Phycita* larva reaches the host prior to the spinning of the cocoon. The walls of infested cocoons are not so hard or thick as those produced by healthy larvae, and this would indicate, also, a certain amount of feeding by the parasite larva while the host was still active.

Undoubtedly the most interesting representative of the family, from the point of view of its host relationships, is an undescribed South African species discussed by Van der Merwe (1921). One to six first-instar larvae were found upon nearly mature larvae of *Dasychira extorta* on the foliage

of fig trees. Feeding is very extensive upon the body fluids of the *Dasychira* larva, and after its death the predator may move to another host. Oviposition has not been observed, but eggs were noted upon cast skins. Apparently, the young larvae do not feed extensively until the host cocoon is spun. Following this, there ensues a rather long resting period, after which either the host larva or the pupa is quickly consumed. The mature larva measures 25 mm. in length. The larval period ranges from 6 to 12 months and the pupal period from 18 to 30 days. Adults appear in the field mainly during late summer. This species is quite far advanced toward obligate parasitism, as indicated by the ability of some individuals to attain maturity upon a single host, though its present tendency to move, if necessary, to a second host classes it more properly as a predator.

Euzophera cocciphaga Hamp., is recorded by Ayyar (1929) as a predator upon the eggs and young larvae of the giant monophlebine coccid, *Aspidoproctus xyliae* Gr., which infests the rain trees of India. The greenish-yellow eggs are deposited singly on the dorsum of the host, most frequently in the posterior region. The newly hatched caterpillar crawls about over the scale for a time and eventually finds its way beneath the body. One to three larvae may be found beneath each scale. Very soon after the commencement of feeding, they securely fasten the margins of the scale insect to the substratum with numerous strands of silk. This is stated to serve the purpose of preventing emergence of the host larvae after hatching. It was noted that no larvae ever emerged from parent scales known to be infested, and yet when a passageway was made through the silken barrier they emerged in numbers. The mature larva of the parasite is grayish-green in body color and about 6.5 mm. in length. Pupation takes place within a tubular cocoon beneath the remains of the host. Other Indian species of this genus are recorded as fruit feeders or stem borers.

Laetilia coccidivora Comst. is a common predator upon the terrapin scale, *Lecanium nigrofasciatum* Perg. (Simanton, 1916*a*), and is known to attack others also, particularly *Pulvinaria, Ceroplastes,* and *Icerya.* The eggs of the first brood are deposited singly among the mature scales during early June, and feeding is principally upon the gravid females. A delicate silken tube is constructed from scale to scale, and pupation takes place within it. The larvae of the second brood feed upon the young scales during late summer. *Vitula saissetiae* Dyar is predaceous upon *Saissetia* sp. in Panama, and the larvae of *V. edmandii* Comst. of North America have been taken in bumblebee nests, though the exact relationship has not been determined.

Cereobata coccophthora Turn. is predaceous upon *Eriococcus*, and its habits, including the provision of a dorsal shield, are quite similar to

those of *Eublemma* of the Noctuidae. *Cryptoblabes gnidiella* Mill., which is normally a foliage feeder upon a variety of plants, has been noted to feed extensively upon the various stages of *Aleurocanthus* spp. in Malaya.

PYRAUSTIDAE

The one member of the family that is well-known because of its predaceous habit is *Dicymolomia julianalis* Wlk. which preys upon the eggs of the bagworm, *Thyridopteryx ephemeraeformis* Haw., in North America (Gahan, 1909). Up to 30 per cent of the bags have been found infested, and a single larva consumes the entire egg contents. The cocoon is spun at the free end of the bag. The normal habit of this species is said to be that of a scavenger in the heads of *Typha*. Balduf (1937) considers that this species, in spite of its very frequent occurrence in bagworm cases, is not essentially predaceous, but that the eggs are destroyed incident to the preparation of a hibernaculum.

CHRYSAUGIDAE

The only information regarding the entomophagous habit in this family relates to *Sthenauge parasiticus* Jor. which is predaceous or possibly definitely parasitic, upon the caterpillars of *Automeris* and *Dirphia* in Brazil (Jordan, 1926). The eggs are presumably laid directly upon the host. The larva spins a silken web transversely across the dorsum of a segment from spiracle to spiracle, forming a tunnel open at both ends. Feeding takes place upon the body spines that border the tunnel, and eventually the host sickens and dies. Individuals have been observed to feed upon dead caterpillars, even boring into the body.

NOCTUIDAE

The genus *Eublemma* contains the principal representatives of the family that are predaceous in habit, though a few species of *Catoblemma* and *Cerynea* have the same food source. They feed quite generally upon all stages of lecaniine Coccidae, particularly those which deposit large numbers of eggs in a chamber beneath the parent scale. The genera most commonly attacked are *Saissetia, Ceroplastes, Lecanium, Laccifer*, etc. Attack has also been noted upon *Philippia, Pulvinaria, Anomalococcus, Eriococcus, Margarodes*, and *Pseudococcus*.

Eublemma scitula Ramb. has been recorded as a predator upon many species of Coccidae in various parts of the world. It is considered to be an important enemy of *Pulvinaria* in India. Rouzaud (1893) states that the larvae feed mainly upon nearly full-grown host scales of *Saissetia*, whereas Balachowsky (1928) states that they are strictly egg feeders. *E. cocciphaga* Meyr. is said to feed principally upon the immature scales upon the foliage and twigs. The larvae of these species have the habit

of covering the body with a light silken web to which numerous host remains become attached (Fig. 213), and this serves as a shield which is carried about as they move from place to place. This shield is stated to constitute a protection from ants. *E. amabilis* Moore is a serious pest of the lac insect in India (Misra, 1924; Misra *et al.*, 1930), and its feeding habits are quite similar to those of *Holcocera pulverea* Meyr., upon the same host. Pupation takes place within the larval tunnel, whereas in the free-living *E. scitula* and *E. cocciphaga* it occurs *in situ* beneath the shield-like covering, which is fastened at its margins to the leaf or twig surface. As many as six generations annually are recorded in India, though two is the more common number for species observed in temperate sections. The feeding habit of the Javanese *E. rubra* Hamp. is described by Jacobson (1913). The shield is moved forward to cover the *Lecanium* individual, and its margin is then fastened to the twig with silken strands. Having thus ensured itself from molestation, the caterpillar proceeds to tear a hole in the dorsum of the scale and devour the body contents. *Catoblemma sumbavensis* Hamp. carries a similar shield and attacks *Laccifer* in the same way.

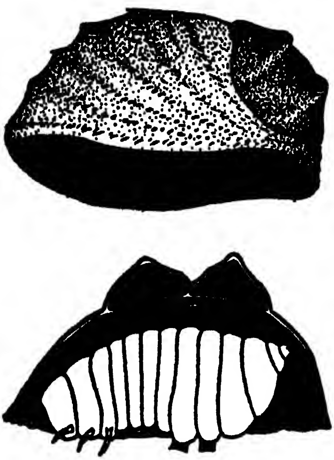


FIG. 213.—A predaceous caterpillar, *Eublemma scitula* Ramb. Above, the portable silken case of the mature larva, bearing the remains of one coccid host and, below, a mature larva within its case. (*Redrawn, after Rouzaud*, 1893.)

In all the cases noted, the eggs are deposited singly or in clusters either upon the host scales or in their immediate vicinity. In *E. amabilis*, they are placed only upon scales that have begun the secretion of the waxy covering. Those of different species have been described as yellowish, brown, or blue-black in color, and they have a distinct surface sculpturing.

The larvae of a considerable number of plant-feeding species of the family have a pronounced cannibalistic tendency, and *Heliothis dipsacea* L. is recorded as being a frequent predator upon the pupae of *Ascia rapae* L. in California.

STREPSIPTERA

The order Strepsiptera, comprising a few hundred species long included in the family Stylopidae among the Coleoptera, is of extreme interest from several points of view. There is a striking sexual dimorphism in the adults, the males having branched antennae, large eyes, paddle-shaped mesothoracic balancers, and large metathoracic wings, whereas the females are apterous and larviform. In all families except the primitive Mengenillidae, the adult females that have been described lack legs, are incapable of ordered movement, and never leave the body of the host. The first-instar larvae, which are known as triungulinids, are of the planidium type and bear a striking resemblance to those of the Ripiphoridae and certain Meloidae. Taxonomically, the order is considered by some authors to be closely allied to the Ripiphoridae, and the free-living females of *Eoxenos* and *Mengenilla* bear a marked resemblance to the aberrant genus *Ripidius* of that family. All species, so far as known, complete larval development within the body of the host in a manner similar to that of *Ripidius* in cockroaches, whereas the Ripiphoridae attacking hymenopterous larvae are external except for a period during the first stage. Early entomologists were greatly confused regarding the females of this order; they were at first supposed to be the larvae of primary parasites of wasps, and the triungulinids in the body were believed to be secondary parasites (Westwood, 1836 '39). The early descriptions of species were based upon the adult male, and it was not until some time later that these active winged creatures were associated with the grub-like females in the bodies of wasps.

Due to their minute size, great activity, and brevity of life, the adult males are not encountered nearly so often by collectors as are the females. A great many species are consequently described upon the basis of one sex only. The definite association of the adults of the two sexes of a species is possible only by rearing, preferably from the same host individual or from those of the same colony. The members of the order have come to be known under the common name of "stylops" from the original generic name of the entire group, a parasitized host is said to be "stylopized," and parasitization by a member of the order is referred to as "stylopization."

HOST PREFERENCES

Parasitization by Strepsiptera has been recorded in four orders and in the families listed below:

Orthoptera
- Gryllidae
- Locustidae

Hemiptera
- Pentatomidae

Homoptera
- Fulgoridae
- Cicadellidae

Hymenoptera
- Sphecidae
- Larridae
- Vespidae
- Mutillidae
- Eumenidae
- Formicidae
- Halictidae
- Panurgidae
- Andrenidae
- Hylaeidae
- Apidae
- Psammocharidae

The records of attack upon Orthoptera and Hemiptera are very few, whereas both the Fulgoridae and Cicadellidae frequently serve as hosts. The great bulk of the host records for the order, however, are of Hymenoptera, particularly of the families Andrenidae, Vespidae, and Eumenidae.

Extended host lists or summaries of host preferences have been presented by Pierce (1909, '18), Robertson (1910), Salt (1927*b*), Salt and Bequaert (1929), and Ulrich (1933). In general, the hosts of the different families, based upon the classification and records given by Pierce, are as follows:

Family	Host Groups
Mengenillidae	Unknown
Mengeidae	Unknown
Stichotrematidae	Orthoptera: Locustidae
Callipharixenidae	Hemiptera: Pentatomidae
Myrmecolacidae	Hymenoptera: Formicidae
Stylopidae	Hymenoptera: Various families
Hylecthridae	Hymenoptera: Hylaeidae
Xenidae	Hymenoptera: Various families
Triozoceridae	Homoptera: Cicadellidae
Halictophagidae	Homoptera: Cicadellidae, Fulgoridae
Elenchidae	Homoptera: Cicadellidae, Fulgoridae

The classification of the order is, however, in a confused state; it is quite possible that a more thorough study, with the accumulation of additional host records, will appreciably modify the above host groupings. Pierce believed that each species is confined to a single host species, and each tribe to a family, though more recent writers have not supported this conclusion. Certainly the assumption of specificity in host preferences throughout the family is not in accord with the findings with respect to other groups of insect parasites that have been studied more extensively. Most instances of presumed specificity are not substantiated after thorough study. Many of the cases that are apparently established beyond reasonable doubt are attributed to the absence of

species closely related to the host in the area of collection. That all of the Strepsiptera, or even a considerable proportion of them, should be specific appears improbable. An experimental study of this subject could be made with very little difficulty. As opposed to Pierce's conclusion, Bohart (1936) has recently found that many species of *Stylops* are parasitic in two or more similar species of *Andrena*.

As a whole, the order may well be considered as beneficial rather than harmful, primarily because of attack upon Fulgoridae and Cicadellidae,

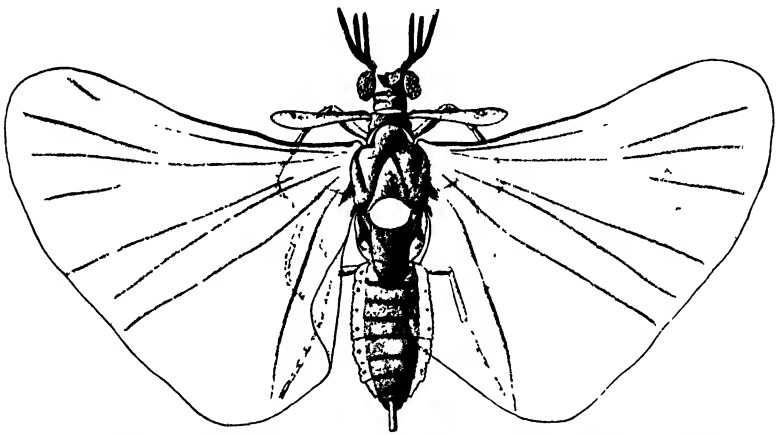


Fig. 214.—The adult male of *Eoxenos laboulbenei* Pey. (*From Parker and Smith*, 1934.)

many species of which are major crop pests. Muir (1906) records that more than 70 per cent of *Perkinsiella vitiensis* Kirk. on sugar cane in Fiji were parasitized by *Elenchoides perkinsi* Pierce (*Elenchus tenuicornis* Muir), and 30 per cent of *Idiocerus atkinsoni* Leth. in India contained *Pyrilloxenos compactus* Pierce (Subramaniam, 1922). It is difficult to evaluate the effect of parasitization of the predaceous Hymenoptera by the Strepsiptera. Schrader (1924), in her discussion of *Xenos* (*Acroschismus*) *wheeleri* Pierce as a parasite of *Polistes*, states that the number at first attacked in a nest is low but that this eventually builds up until it brings about the virtual extinction of the colony. Piel (1933*b*) reports a parasitization of 25 per cent of *Sphex nigellus* Smith by *Ophthalmochlus* sp., and Theobald has recorded 50 to 70 per cent parasitization of *Andrena* by *Stylops* sp. The records of attack upon honeybees are very few, and members of the order are apparently only occasional parasites of this valuable insect (Beljavsky, 1926). The highest and most consistent parasitization is that recorded by Kirkpatrick for *Corioxenos antestiae* Blair upon the pentatomid, *Antestia lineaticollis* Stal., a serious pest of coffee in East Africa. Here the portion attacked ranged from 12 to 84 per cent during the year, with an average exceeding 40 per cent.

The only attempt to utilize representatives of the order in biological control has been in Hawaii, where several species from various parts of the world were imported in the effort to control the sugarcane leafhopper, *Perkinsiella saccharicida* Kirk., though none of them became established.

BIOLOGY AND HABITS

The most detailed accounts of the biology and habits of the Strepsiptera are the outstanding contributions by Nassanov (1892, '93), followed by those of Brues (1903, '05), Perkins (1905*c*), Pierce, (1909, '11, '18), Wheeler (1910), Smith and Hamm (1914), Schrader (1924), Schultze (1925), Ulrich (1927, '30, '33), Parker and Smith (1933*b*, '34), and Kirkpatrick (1937*b*). Nassanov's articles have been translated into German by Sipiagin and published, with comments and additional notes, by Hofeneder (1910). An extended account of the internal anatomy of the immature stages and the adults of *C. antestiae* Blair has recently been given by Cooper (1938).

Reproduction.—Reproduction in the Strepsiptera is consistently larviparous; and, in view of the manner of development and the position of the adult females, it seems extremely improbable that any species will be found to deposit eggs. There appears to be no difference in this respect between the forms having free-living females and those which are confined in the body of the host.

The few figures available indicate a uniformly high reproductive capacity; this is essential because of the hazards encountered by the triungulinids before they reach the host, which must result in a very high mortality. Newport records rearing more than 7,000 triungulinids from a single female of *Stylops aterrima* Newp.; this is the highest figure thus far given for the order. Pierce counted 2,252 in one female of *S. swenki* Pierce, "omitting all consideration of multitudes of undeveloped eggs." Several thousand progeny are mentioned for *Xenos wheeleri*, *X. auriferi* Pierce, and *Eoxenos laboulbenei* Pey., and *Pyrilloxenos compactus* is said to produce more than one thousand.

Extended studies upon oogenesis and embryology in members of the order have been made by Brues, Hoffman (1913), Schrader, and Noskiewicz and Poluszynski (1928). The latter authors (1924) give a brief account of supposed polyembryonic development in a species of *Halictoxenos* parasitic in *Halictus simplex* Per. The information presented is not conclusive.

The entire brood of a single female emerges from the body in a surprisingly short period of time, usually all in a single day, and Parker and Smith state that several thousand triungulinids of *E. laboulbenei* emerged from one female in less than one minute. Subramaniam (1922, '32)

mentions that the triungulinids of *P. compactus* and *Trydactylophagus mysorensis* Subr. "shot out into space" through the opening on the ventral side of the cephalothorax. Exit from the body of the parent *Eoxenos* is through the genital opening on the venter of the seventh abdominal segment, whereas in the forms having apodous females the triungulinids first pass through the genital ducts into the brood chamber and thence to the outside through the genital opening between the head and thorax. Kirkpatrick states that many of the triungulinids of *Corioxenos* emerge through the oral aperture of the head. The membrane covering the genital opening is perforated at the time of mating, and this provides the normal point of exit in most species.

It may be pointed out that the use of the term "larviposition" in respect to reproduction in this family is inexact, for it implies an act on the part of the female. So far as known, this is not true in the Strepsiptera, and the triungulinid leaves the body of the parent female entirely of its own volition and unaided by any act of the latter or stimulus provided by it.

Various authors have emphasized the simultaneous development of all eggs within the body of the female and the short period required for the emergence of the entire brood of triungulinids. This is undoubtedly true of the great majority of species, but a markedly different course of events takes place in the case of *Corioxenos antestiae.* Females of this species have been found by Kirkpatrick to produce young over a period of more than three months. One individual produced 3,720 in 95 days, with 134 remaining within the body at death, and another 2,220 in 49 days. Under laboratory conditions, a female produces an average of about 50 triungulinids per day. In general, the females of this species continue to produce progeny until the death of the host. In spite of the protracted period of reproduction, only a single mating is necessary during the lifetime of the female. No instance was found of spermatozoa being present in the body more than 18 days after mating, and consequently embryonic development may cover a minimum period from fertilization to emergence of 6 weeks and a known maximum of about 19 weeks.

Activities of the Triungulinid.—Considering the extended studies that have been made upon the biology of the family, there is very little information yet available regarding the activities of the triungulinids from the time of emergence from the body of the parent female until the host stage in which development is to take place is reached. They undoubtedly leave the maternal host in a relatively short time, particularly if this is a homopteran. The jumping habit of the triungulinids, which is common to the planidia of several orders, was first noted by Saunders in 1853. In *E. laboulbenei,* jumping is accomplished in a

rather unusual way, the abdomen being raised from the substratum and the caudal cerci brought forward beneath the body, following which the body is suddenly straightened out, projecting the insect into space.

The triungulinids of several species are stated to be positively phototrophic; this is an aid in attaining a position in which contact with a carrier or host may be made. In *Corioxenos*, it has been shown that relatively little movement of the triungulinid takes place, and apparently no searching; the triungulinid is consequently dependent upon direct contact to reach the host. The waiting or alert position, which may be held for hours, is quite characteristic, the terminal cerci being bent forward under the abdomen and the anterior end of the body considerably raised and supported only by the hind legs. This is in marked contrast to the habit of the planidia of other orders, which stand erect upon the caudal sucker, with the body braced only by the caudal cerci. Jumping, in the case of *Corioxenos*, takes place as a result of the stimulus provided by a near-by moving object, and particularly in response to certain colors. Those which are most attractive are red, black, and orange (Kirkpatrick, 1937*a*). It is worthy of note that the last two are the predominant colors of *Antestia*, the normal host. In case the object to which the triungulinids become attached is not an immature *Antestia*, they leave at the first opportunity, whereas if it is an *Antestia* they make their way to the dorsum of the thorax and abdomen, between the coxae or between the head and thorax, where they cling immobile, with the mouth parts and legs, until the next molt of the host.

Though penetration into the host by this species normally takes place at the time of the host molt, yet it has been demonstrated that triungulinids will readily enter adult hosts bearing mature *Corioxenos* of either sex. In such cases, entry is effected at the point of extrusion of the older parasite. It is quite probable that a second generation of parasites can develop to maturity in *Antestia* provided that the number of individuals is not so high as to bring about premature death.

Species that develop in Homoptera reach the host directly, without the intervention of a carrier, for the triungulinids are released on the foliage frequented by nymphs and adults of the host. These insects are often so exceedingly abundant that the chance of a triungulinid reaching a host directly is very good. With hymenopterous hosts, however, the aid of a carrier is very probably customary, though possibly not essential. The larva within the cell, rather than an active stage of the host, must be reached. The bees and wasps that are subject to attack by Strepsiptera have two general methods of feeding and caring for the brood, and these have a bearing upon the chances of the triungulinids reaching the larvae: (1) The food is stored in the cell, the egg deposited upon it, and the cell then sealed; or (2) the egg is first laid in

the cell and the larva fed periodically until maturity is attained, after which the cell is closed. It is evident that, in the first case, the period in which entry into the cell is possible is very short, probably not more than one day, and consequently such species are probably only lightly attacked. This omits, however, the possibility that the triungulinids may be able to penetrate the cell after it is closed. If entry is on the day the egg is laid, the triungulinids are under the necessity of waiting for a considerable time until the egg has hatched and the larva is sufficiently developed to withstand attack. Owing to the small size of the triungulinid in relation to the host, its penetration into the first-instar larva may be possible without serious injury to it. In the second case, the cell remains open throughout the larval feeding period, and the larva is tended one or more times each day by the adults, so that the opportunities for parasitization are much greater.

Though it is doubtless true that some triungulinids transfer directly from the maternal host in the nest, yet this is not believed to be of common occurrence, for parasitized females do not engage in nest building, at least not at the time of escape of the parasite brood. Pierce considers that transfer is effected mainly upon blossoms and at other places frequented generally by the bees and wasps. The possibility of transfer taking place upon blossoms was first presented by Westwood in 1839. In the case of hosts of social habit, there is an excellent opportunity for transfer by direct contact in or near the nests, in contrast to the improbability of such an occurrence among the solitary species.

Few definite observations have been made regarding the manner of entry of the triungulinid into the host body, or the point at which penetration takes place. This is always accomplished in the first stage, and advanced triungulinids of several species have been dissected from hymenopterous larvae. They apparently lie free in the body cavity. Saunders (1853) placed triungulinids with nearly full-grown *Polistes* larvae and noted that penetration took place very soon thereafter. Dissection one week later revealed the larvae just undergoing the first molt. Kirkpatrick frequently observed the entry of *Corioxenos* into its pentatomid host; this usually takes place on the pronotum at the time of molting and is accomplished within 20 to 30 minutes of the beginning of the molt. Though entry may take place at any molt of this host, yet it is most successful at the first three. Rather surprisingly, the newly hatched nymph is never attacked, even though in physical condition it is much the same as at the time of the following molts. Possibly, it will be found that the species attacking Fulgoridae and Cicadellidae likewise enter the host body only at the time of molting.

Kirkpatrick has called attention to the apparent immunity of certain deformed *Antestia* to parasitization by *Corioxenos*. A portion of the

older nymphs are found to have malformed antennae, and rearing experiments, in which these were subjected to attack by triungulinids of the parasite, showed that very few effected entry into the body. Only 18 out of 54 triungulinids entered the bodies of these individuals, and only 8 of 49 hosts were successfully parasitized. This is in marked contrast to results secured with normal hosts, among which well over 90 per cent were successfully parasitized when exposed in the same way. It is thought that a deficiency in the molting fluid, resulting in a difficult molt, may be responsible for the malformed antennae. If this fluid provides the stimulus for penetration by the parasite, as is considered probable, then such a deficiency would reduce the stimulus to the point where the triungulinids would not react to it, and, as a consequence, these deformed individuals would largely escape parasitization.

Larval Development.—Detailed information regarding the habits of the intermediate larval stages is lacking except in *C. antestiae*. If penetration into the host body is accomplished in the thoracic region, migration of the parasite larva to the abdomen usually takes place late in the second stage. From this point onward, there is little movement until that incident to the extrusion of the cephalothorax. In hymenopterous hosts, also, the larvae migrate to the abdomen during the early period of their development if entry has taken place in the anterior portion of the body, and probably while the host is still in the larval stage.

Earlier authors mention only three larval instars; but Nassanov, Schrader, and Kirkpatrick found that there are probably seven (Schrader states that the males have only six larval instars), and their more precise observations would indicate that this number is more nearly correct. In molting, a transverse break occurs across the anterior end of the body, and the larva then wriggles out of the exuviae. Feeding is chiefly by diffusion through the integument, though in *Corioxenos* movements of the rudimentary mouth parts were noted, but it is uncertain whether this represents direct feeding. Smith and Hamm have examined the alimentary system of *S. melittae* Kirby and found it to be degenerate and functionless.

The sex of the larvae can be determined at a comparatively early stage of development, there being appreciable differences in the third instar. Extrusion of the cephalothorax from the body of the host occurs, in both sexes, during the seventh stage. Species that attack Hymenoptera extrude the cephalothorax during the pupal stage of the host or after it has transformed to the adult stage but before the integument has hardened. In pentatomid hosts, this occurs only after the adult stage is reached, but in the Homoptera it may take place while the host is still in its nymphal stage. In the majority of cases where the orienta-

tion of the cephalothorax has been noted, that is, in *Xenos*, *Stylops*, and *Elenchoides*, it has been found that the side of the cephalothorax in contact with the host body is the dorsum, the venter being the outer, exposed side. Saunders, however, states that the reverse is true in the case of *Stylops* sp. and *Hylecthrus* sp., and Kirkpatrick shows that *Corioxenos*, also, normally lies with the dorsum as the exposed side. In each species, the orientation of the two sexes is the same. This difference in orientation among the different species is probably correlated with the position of the larva in the body of the host. In *Corioxenos*, the mature larva lies with its venter against the body wall of the host, and in effecting emergence the cephalothorax is curved ventrally so that when the process is complete the body is U-shaped, the dorsum being outward with respect to the host body. In other species, for the inverted position to be taken the larvae must take the same internal position with respect to the host body wall, but they lie with the cephalothorax and abdomen in the same plane and effect extrusion by a series of forward thrusts. The female of *Dacyrotocara undata* Pierce (Fig. 215) is found in the latter position, the body being straight and cylindrical, and the first abdominal segment extends forward far beyond the apex of the cephalothorax.

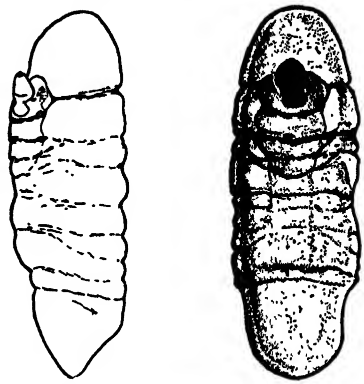


Fig. 215.—The adult female of *Dacyrtocara undata* Pierce, lateral and ventral views. (*From Pierce*, 1918.)

Among the species that develop in Hymenoptera, the cephalothorax of the parasite is extruded through the intersegmental membrane of the abdomen at any point on the periphery, though a greater number are found dorsally than ventrally or laterally. The natural curvature of the abdomen of the wasp or bee, with the dorsum markedly convex, permits of more ready extrusion in that area. The cephalothorax of the parasite is always directed caudad, a position induced by the overlapping of the abdominal segments of the host. Those of the males are usually found overlying the third segment, whereas those of the females are generally on the fifth segment. They may, however, be found on any of the other segments with the exception of those comprising the genital system. The point of extrusion of the cephalothorax of the species attacking Hemiptera and Homoptera appears to present a greater consistency within each species than is the case with those infesting Hymenoptera. In *Corioxenos*, the cephalothorax of both sexes is extruded dorsally through the intersegmental membrane between the third and fourth abdominal tergites. That of the male is found on the median line, or

near it, whereas that of the female is invariably found near the lateral margin (Fig. 216). Those upon Fulgoridae are quite regularly upon the pleural region only, whereas the species attacking Cicadellidae are found in either the dorsal or the ventral position (Perkins, 1905c). This author states that those of the males of *Halictophagus* are found either dorsally or ventrally, whereas those of the females are in the pleural region only. According to Pierce, the males of *Stenocranophilus quadratus* Pierce are usually situated on the fifth segment of *Stenocranus*, and almost invariably dorsal in position, whereas the females are on the third segment and usually lateral. In *Tettigoxenos orientalis* E. & H.,

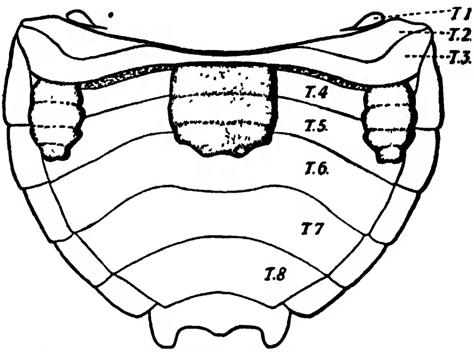


FIG. 216.—Diagram of the abdomen of *Antestia*, showing two female and one male (center) *Corioxenos antestiae* Blair in characteristic position. (*From Kirkpatrick*, 1937.)

the great majority are ventral and located on the fourth or fifth segments of the adult hosts and on the third segment of the nymphs. In general, it appears that in hymenopterous hosts the point of extrusion of the females is farther back than that of the males, whereas in the Homoptera the opposite is true. Pierce considers this condition to be due to the fact that the female parasites are larger than the males in the first case and smaller in the second.

Pupation.—In all species having apodous females, the individuals of this sex transform to the adult stage directly from the seventh-instar larva without an intervening recognizable pupal stage. The male, however, undergoes a complete metamorphosis in which the pupa develops within the seventh larval exuviae *in situ* in the body of the host. It may not completely fill this "puparium," and in some instances the body is withdrawn from the cephalothorax so that it lies entirely within the host body. The adult male may remain within the puparium for several days after casting the pupal skin and it then effects emergence by pushing off the "operculum," or head portion, of the cephalothorax. This takes place during the early morning hours, particularly in bright sunlight. Death of the host prior to this time does not affect the parasite, for

adult males have been reared from hosts that had died nearly a week previously.

In *Eoxenos* (Parker and Smith, 1933*b*, '34) and *Mengenilla quaeseta* Silv. (Silvestri, 1933), which have free-living adults of both sexes, there occurs what is considered to be a pupal stage of the female as well as of the male. The pupa of *Eoxenos* is found within the last larval exuviae, and at emergence of the adult the pupal skin is left almost intact. Occasionally, the female remains permanently within the larval exuviae, in which case the pupal skin is torn into fragments and pushed back into the posterior end. The larval shell remains intact except that the head is detached, and the opening thus made serves as a means of egress for

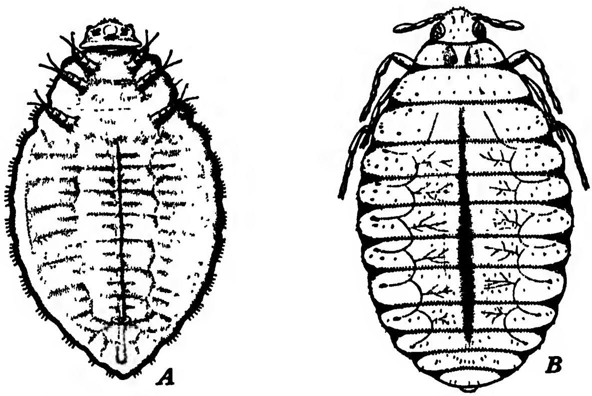


FIG. 217.—*Eoxenos laboulbenei* Pey. *A*, the mature larva, ventral view; *B*, the adult female, dorsal view. (*From Parker and Smith*, 1933.)

the triungulinids. The males likewise pupate within the last larval skin, and at emergence of the adult the head and first thoracic segment are broken off. The pupal shell is usually found within the larval exuviae.

Mating.—The question of whether or not mating actually takes place among the Strepsiptera has been the subject of controversy among a number of authors. Several have cited the apparent scarcity of males to support the conclusion that particular species normally reproduce unisexually; others have stated that the male, while present, is incapable of mating and is in the process of disappearing. The activities of the adult males during their brief span of life, usually less than a single day, are of particular interest. They are greatly attracted to the host insects themselves, and the finding of a host is followed by a search over the body for the female parasite. Attempts at mating have been noted in several species, and Pierce cites several instances where this was apparently successful. That actual fertilization had taken place, however, was not proved conclusively.

Smith and Hamm (1914) came to the conclusion that fertilization cannot take place; their evidence in support of the claim for unisexual reproduction is based on the following points: (1) There is no opening or apparatus in the female adapted for conveying the spermatozoa to the eggs. (2) The eggs remain throughout their development encased in the follicular epithelium of the ovary, so that access to them by spermatozoa which may have entered the body cavity is very difficult to imagine. (3) Parthenogenesis must occur as a normal rule in the parasites of *Halictus*. (4) The known stages in the polar-body formation of *Stylops* are inconsistent with the view that fertilization by a spermatozoon has been effected. (5) Actual copulation by the male has never been adequately observed. It may be mentioned that the fourth item given above was included because the male is exceedingly rare among the species attacking *Halictus*, Perkins having found only one or two among nearly a thousand individuals seen by him.

Perkins (1918*b*) observed copulating pairs of *S. aterrima* and was able to kill them *in situ*. A close examination revealed that the aedeagus was inserted into the brood chamber. Hofeneder (1923) observed *Stylops in copula* on a female of *Andrena flavipes* Perez. for a period of two and one-half minutes. These observations, though corroborative, were not in themselves conclusive, and it was not until the thorough studies by Schrader upon *X. wheeleri* that the apparent mating, as observed by others, was proved to result in fertilization of the eggs. Mating was observed in 10 instances and covered a period of 20 to 50 seconds. In each case, the females were of a certain age, or stage of development, for the cephalothorax had been exserted only four or five days. This very possibly is the explanation of the difficulties experienced by earlier investigators, who may have been using older females that had already been fertilized. The spermatozoa are released through the genital opening into the brood canal and enter the body through the four trumpet-shaped ducts on the venter of the abdomen. They then disperse throughout the body, penetrate the egg membrane, and effect fertilization. A cytological examination of virgin females revealed that the eggs develop as far as the metaphase of the first maturation division, which is reached four or five days after extrusion of the cephalothorax; this condition is maintained for 10 to 14 days, after which degeneration takes place. It is thus demonstrated that not only does fertilization take place but that parthenogenetic reproduction cannot occur in this species. There still remains, of course, the possibility that it may occur among other species but in no instance thus far cited has evidence been presented that points definitely toward such a mode of development. The case of the species attacking *Halictus* is explained as being analogous to that of *Xenos*, in which mating takes place in the autumn and only the gravid females

persist until the following spring. Collections at this time would indicate that the entire population is exclusively of the latter sex.

Kirkpatrick has made extended observations on the mating habits of *Corioxenos.* The male is greatly attracted to the host insect, even if it is unstylopized, and is not at all attracted to females of its own species after they are removed from the host body. It apparently is attracted first to the host by sight and then to the female by touch. In effecting mating, it is first necessary for the male to penetrate the membrane covering the exposed lateral genital opening. In *Eoxenos,* on the other hand, Parker and Smith noted that the aedeagus of the male apparently penetrated the body wall along the median ventral line rather than the genital opening on the seventh segment. If this is the case, there should be no question regarding fertilization of the eggs taking place, for they lie free within the body cavity.

The period of time in which the females remain capable of being fertilized is apparently variable. In *Corioxenos,* mating may take place successfully four to seven days after extrusion of the cephalothorax, but in one instance a female kept in confinement was successfully fertilized 119 days after extrusion.

Life Cycle.—The life cycle, from the time of entry of the triungulinid into the host body to the emergence of the adult male or the beginning of emergence of the new brood of larvae from the body of the female, has been determined for only a very few species. It is exceedingly variable, particularly in those species which attack the host in its immature stages but do not themselves reach maturity until the host attains the adult form. This applies especially to those attacking *Polistes* and other wasps of similar habit which are subject to attack throughout the larval period and to species having pentatomid hosts which are attacked in any nymphal instar but mature only in the adult.

Nassanov mentions that the pupal stage of the male of *X. vesparum* Rossi covers 28 to 32 days, whereas Saunders states that only eight days elapse from the extrusion of the cephalothorax to emergence of the male of *Hylecthrus rubi* Saund. In *E. laboulbenei,* the pupal stage is completed in 12 days. The males of *C. antestiae* complete the cycle from entry of the host to adult emergence in a minimum of 50 days, of which the pupal stage represents about 12 days, whereas the female attains the adult stage in 34 to 36 days, of which 28 to 30 days represents the time from entry of the triungulinid to the extrusion of the cephalothorax.

Hibernation of the species attacking wasps and bees is usually accomplished by the mated females. *Hylecthrus,* however, is said to pass the winter in its early larval stages within the *Prosopis* larvae, this departure being made necessary by the hibernation habit of the host, which takes place in the larval rather than in the adult stage.

The information at hand regarding the cycle of *Eoxenos* indicates that there is only a single generation each year. The adult gravid females are found during the autumn and remain concealed under stones and other objects during the winter. Development of the embryos in the body is not complete until the following spring, and the triungulinids issue from the parent body early in July. This indicates that larval development, in whatever manner it takes place, is completed in a relatively short period of time.

The duration of the various stages in the known parasitic species is governed in part by the factors mentioned above. The triungulinids are adapted to a relatively long period of free life, which is necessary to enable them to reach the proper hosts. This has been measured only in *Corioxenos*, which survives for a maximum of 19 days in the absence of hosts and 34 days if external attachment to the host is effected. The greater portion of this longer period is passed in an entirely inactive condition on the host body while awaiting the molt, and this presumably accounts for the greater length of life. The first molt takes place three to six days after entry into the host body, and a corresponding internal feeding period of one week or less has been noted in other species.

Irrespective of the time of entry of the triungulinids into the host body, the mature larval stage is attained, in hymenopterous hosts, only when the host is approaching the time for transformation to the adult stage. It appears probable, therefore, that the histolytic processes incident to pupation provide the stimulus for the completion of growth. Delay in development until this condition of the host is attained has been shown to be obligatory in several other parasitic groups.

The time of extrusion of the cephalothorax between the abdominal segments of the host, after the transformation of the latter to the adult stage, has been noted in only a few instances. The cephalothorax of *X. vesparum* is extruded from the host abdomen five to eight days after the *Polistes* adults emerge from their cells. In *Stylops* spp. and *Ophthalmochlus* sp. the adult males usually emerge the day the hosts first leave the nest; but this does not aid appreciably in determining the time of extrusion, for the hosts may have been in the adult stage in the nest for a considerable period. According to Pierce, the cephalothorax of *X. pallidus* Brues may not be extruded until several days after the wasp has left its pupal cell. In *Corioxenos*, extrusion takes place not more than 36 hours after the final transformation of *Antestia*. Saunders records observing the activities of male larvae of *Hylecthrus rubi* beneath the abdominal integument of advanced *Prosopis* pupae; extrusion was noted to take place almost immediately after the assumption of the adult form by the host. It is to be expected that extrusion will take place very soon after the pupal skin is cast, for the integument can be more

readily penetrated at this time than after complete hardening has taken place.

SEX RATIO OF HOST AND PARASITE

An extended account has been given by Pierce (1909) relative to the sex ratios of a number of species of Hymenoptera found to be stylopized, the percentage of each sex stylopized, and the sex ratio of the parasites themselves. In 1,553 *Polistes annularis* L. collected during the month of October, only 15.6 per cent were females. Of the above number, 17.2 per cent were parasitized, but the percentage was 19.7 among males and only 2.8 among the females. The sex ratio of the parasite, *Xenos pallidus*, was approximately 1 to 2, the males predominating. Figures are presented for the parasitization of other species of *Polistes*, but for much smaller collections, and these gave results often at variance with the above, particularly with respect to the sex ratio of the hosts. In *Andrena crawfordi* Vier., 43.3 per cent of 266 bees collected were females, and of these 53.1 per cent were parasitized, as compared with only 20.6 per cent of the males. The sex ratio of the parasite showed a slight preponderance of females. Schrader (1924) reports that September rearings of *Xenos wheeleri* from *Polistes* gave a majority of more than 2 to 1 in favor of the males, whereas May and June collections yielded female parasites only. Wheeler's (1910) earlier records on the same species, taken during the latter part of August, showed a male preponderance of nearly 4 to 1. It is apparent that not only does the sex ratio of the host vary widely from one season to another, but the ratios of the parasites themselves differ markedly during the course of the year and in different collections of hosts. Few male wasps survive the winter, and few of those of either sex from which parasites have emerged would be able to do so.

In *Stenocranophilus quadratus*, the males were found to predominate in the ratio of 1.7 to 1, and parasitization of female *Stenocranus* was slightly higher than of the males. Esaki and Hashimoto (1931) found that the females of *Elenchinus japonicus*, parasitic in *Delphacodes*, predominate in the ratio of 2.5 to 1, whereas in *Tettigoxenos orientalis*, parasitizing *Parabolocratus*, the two sexes are present in approximately equal numbers.

In regard to the number of individuals that are able to develop in a single host, the greatest number recorded in a hymenopteran is the 31 larvae of *Xenos* reported by Brues in one larva of *Polistes*. The largest number known to have reached the exserted stage is 15, these being male pupae found in a male of *P. annularis*. Usually, however, the number in each host is between 1 and 5. In homopterous hosts, Esaki and Hashimoto noted 1 to 3 in each individual, and Subramaniam, in his studies on *Pyrilloxenos compactus*, found 1 to 3 in *Idiocerus* sp.

Misra (1917) records a maximum of 7 of this species in nymphs of *Pyrilla aberrans* Kirby and 12 in the adults.

As a result of his studies on several species of *Xenos*, Brues came to the conclusion that there is a marked tendency for all parasites developing in a single host to be of the same sex. Data presented by Pierce on one of the same genus, *X. pallidus* in *Polistes annularis*, show that of 100 male hosts, containing more than one parasite and averaging 2.99, 26 lots were males only, 11 were females only, and 63 were of both sexes. The disparity between the number of pure colonies of the two sexes is largely explained by the predominance of the males in the sex ratio of the parasite. Wheeler's studies on *X. wheeleri* showed an average of 2.4 individuals developing in *Polistes* sp.; the maximum was 11. He states that in all instances where the number was in excess of 4 all of them were of the same sex. This implies a differential death rate among the larvae of the two sexes, the males dominating because of their smaller size and much lower food requirements. Schrader (1924), in dealing with the same species, corroborates Wheeler's conclusion regarding the differential death rate among the larvae; and dissections of larvae, pupae, and adults of *Polistes* showed that the larvae of the two sexes of *Xenos* were present in approximately equal numbers. Vandel (1932) presents figures for *X. vesparum* in *P. gallicus* L., in which it is shown that 18 out of 31 wasps containing more than one parasite bore one sex only, of which 16 were male broods. In 13 mixed broods, 9 contained an excess of males, the numbers were equal in 3, and only 1 contained an excess of females. It should be noted, however, that 21 out of 25 solitary individuals were males. Piel's limited observations on *Ophthalmochlus* sp. in *Sphex* showed the males to be in the minority in mixed broods. The figures presented in the above instances do not indicate any consistency in the order as regards the tendency toward a preponderance of males in mixed broods. Other species attacking Hymenoptera for which data are given are not represented in sufficient numbers to permit of a conclusion on this point.

The most detailed information regarding the sex ratio is available in the case of *Corioxenos*, of which 1 to 5 develop in each host individual. Field-collected material numbering 1,000 hosts showed that 47.7 per cent bore only a single parasite, and among these the females predominated in the ratio of 1.5 to 1.0. This may be considered as the normal sex ratio of the parasite. In the case of hosts containing two parasites, the female preponderance was greater, the ratio being 2.4 to 1, whereas with a greater number in each host the sexes were present in approximately equal numbers. These records show no tendency for the brood in a host to be of one sex only. Of 249 *Antestia* containing three or more extruded

Corioxenos, 16 of the broods were pure male, 9 were female, and 224 were mixed.

EFFECTS OF STYLOPIZATION UPON THE HOST

Parasitism by Strepsiptera brings about many noticeable changes in the host, among which are various internal changes due to the feeding of the larvae and often a decided influence upon the primary and secondary sexual characters of the adult host. Many of these result from an upset of the nutritional balance of the host due to feeding by the parasite. The more extended studies of the effect of stylopization have been by Perez (1886), Pierce (1909), Wheeler (1910), Smith and Hamm (1914), Perkins (1918*a*), and Salt (1927*a*, '31*a*).

One effect that is quite noticeable in various bee and wasp hosts is an acceleration or retardation in development to the adult stage. It was pointed out by Westwood in 1840 that parasitized *Andrena* adults appear about one month earlier in the spring than do the healthy adults, and Saunders also noted earlier emergence in the case of *Prosopis*. Pierce records that the first adults of *A. crawfordi* found in the field were parasitized to the extent of 59 to 79 per cent whereas those taken a few days later showed a much lower figure. Wheeler found only adult *Xenos* in *Polistes* wasps of the autumn broods, and these parasitized individuals were considered to belong to earlier broods that had been retarded in their larval and pupal development. This implies that there is only a single parasite generation each year, though Schrader later demonstrated that there are two. This author noted that the host larvae and pupae which remain longest in the nest are the most heavily parasitized and that their random distribution in the nest indicates an actual retardation. From the evidence at hand, it thus appears that there is an actual acceleration in development among the bees in contrast to a retardation among the wasps. Such effects of parasitism are known to occur commonly among other insects. Salt (1927) has given what appears to be a logical explanation of this apparent discrepancy. Because of the presence of the parasite in the body of the host larva and its continuous abstraction of food materials from the blood, the host is kept in a state of continual hunger. As a result, stylopized bee larvae feed more rapidly and consume the food supply in the cell earlier than the unparasitized individuals, and consequently pupate and emerge at an earlier date than do the unparasitized individuals. In *Polistes*, however, the food supply is not limited in quantity, and the larvae are presumably provided with food as long as they require it. The parasitized individuals have the same persistent hunger as is found among the bees but are able to continue to feed sufficiently to compensate for the materials abstracted by the

parasite. This results in the larval stage being prolonged, and adult emergence is correspondingly delayed. In the Fulgoridae, which are able to secure whatever added food is required, the parasitized individuals likewise show a retardation in development.

It has been pointed out by several authors that parasitism by male Strepsiptera results in greater injury, and brings about more profound changes in the host, than does that by the females. It should be noted that many of these changes are brought about while the host is in the mature larval and pupal stages; consequently, the abstraction of large quantities of food materials from the body for the production of eggs by the parasite female is not involved. At the time of emergence of the parasitized adults, the male parasite is a more highly organized body than the female and has been more of a drain upon the vitality of the host. This explanation is not in accord with that given for the preponderance of males in heavily parasitized hosts, which is attributed to a differential death rate whereby the males dominate because of their smaller size and supposedly lower food requirements.

There is generally a marked loss of vitality among parasitized host adults, ranging from merely reduced activity to a more or less complete cessation of normal functions. Parasitized male bees and wasps have been observed to mate apparently normally, and this is occasionally the case with females, also. The females among these hosts seldom attempt to carry pollen or to build or furnish nests. In *Andrena*, some species, when parasitized, never carry pollen, whereas others, and *Chloralictus*, also, may do this occasionally or frequently.

Injury to the internal organs of the host is often very severe and is brought about indirectly through the abstraction of food from the blood rather than by direct feeding and consequent laceration of tissues. All authors are agreed that atrophy of the ovaries is so far advanced as completely to prevent the formation of mature eggs by parasitized females, a condition first pointed out by Kirby in 1828. Newport records that the secretory and poison glands of *Andrena* are reduced, the tracheal system is reduced and with the vesicles few and imperfect, the nerve ganglia of the abdomen are atrophied, and the intestine is empty and dislocated. Most authors have concluded that the male reproductive system is unimpaired, though Perez mentions that these organs are atrophied only on the side bearing the parasite, and Salt noticed a slight reduction in size. An exception to the above generalization occurs in *Antestia* spp. parasitized by *Corioxenos antestiae*, in which the great majority of the males proved to be sterile, as determined by breeding experiments with unparasitized females, even though apparently normal spermatozoa were present in all specimens examined and mating apparently took place normally. Functional sterility may be more general

than is now thought. Among the females that are parasitized at the time of the final molt and that contain only a single parasite, a small number, in the neighborhood of 1 per cent, contain 5 to 15 apparently mature eggs each. In spite of this, however, no such female ever accomplished oviposition.

Death of the host is by no means an invariable result of parasitism by Strepsiptera. Perkins and Misra have pointed out that death of parasitized leaf hoppers usually follows shortly after emergence of the male parasite, this being due to the empty puparium providing a large opening into the body cavity through which desiccation of the viscera takes place and which also serves as a point of entry of disease organisms. The female leaf hoppers containing parasites of that sex merely become sluggish at the time of release of the triungulinids and may live for a considerable time. Perkins believed that the presence of a fungus disease is essential to fullest effectiveness of these leaf-hopper parasites. In view of the injury to the reproductive system of the female hosts, this would seem to be of no consequence; for reproduction has ceased, and these individuals cannot contribute further to the increase of the population. In the case of *Antestia* spp., adults containing either male or female *Corioxenos* live very nearly as long as healthy individuals. Pierce and others have shown that adult *Polistes* bearing empty male puparia may live for a considerable time and may even be able to hibernate successfully.

A great deal of interest has been attracted to the subject of external changes brought about as a result of parasitism by Strepsiptera. The first extended study on this phase of the problem was by Perez upon a large number of species of *Andrena*, followed by those of Pierce, Wheeler, Smith and Hamm, and Salt. Aside from mechanical distortion and occasional direct injury induced by the extrusion of the cephalothorax of the parasite, the general external changes are evident in the relative size of the parts of the body, the integument, puncturation, pilosity, and wing venation. The principal secondary sexual characters that are affected, with the direction of the changes that take place, are as follows:

Antennae—color and proportionate length of segments.
Pubescence—color.
Pollen-collecting apparatus—size of tarsi and number of bristles.
Clypeus—color and shape.
Mandibles—color.
Genitalia—size, shape, and proportions of parts.

It has been determined that in *Polistes* no appreciable modification in secondary sexual characters results from parasitism, whereas the most marked changes are found in *Andrena*. In the latter genus, Perez concluded that the modifications constitute actual inversions of develop-

ment. "The stylopized *Andrena*, male or female, is not merely a diminished male or female; it is a female which takes on male attributes; a male that takes on the characters of the female." This conclusion has been corroborated by later investigators. The changes are so pronounced that in a considerable number of instances parasitized individuals have been described as new species, a practice that has resulted in much confusion.

Salt has pointed out that there is no uniformity in the effect of stylopization upon the external characters of hymenopterous hosts. Even among individuals of a single species, the differences may be very great, probably owing to a variation in the stage of development at which parasitization takes place. In some cases, particular effects are revealed in only one sex. The above differences are correspondingly greater between species and genera. One point which is emphasized is that the various changes occur in a definite order.

Among the Fulgoridae, Esaki and Hashimoto (1931) found a marked "neutralization" of the genitalia of both sexes of *Delphacodes furcifera* Horv. as a result of parasitism by *Elenchinus*, whereas no such effect was evident in the cicadellid, *Parabalocratus prasinus* Mats., parasitized by *Tettigoxenos*. Kirkpatrick observed no changes in the secondary sexual characters of the pentatomid, *Antestia* sp., as a result of attack by *Corioxenos*.

IMMATURE STAGES AND THE ADULT FEMALE

The Egg.—The fully developed eggs in the body cavity of the female are minute and almost spherical in form and usually have the chorion thin and membranous. That of *E. laboulbenei* is 0.07 mm. in diameter and, in its early stages, is seen to have a band of irregular hexagonal cells extending around it. These are not surface markings, however, but represent the developing embryo. In some species, at least, there is an increase in size during incubation, and just prior to hatching the larva lies in a curled position, with the posterior portion of the abdomen sharply bent ventrally beneath the body.

The Larval Instars.—The first-instar larva of the Strepsiptera is generally referred to as a triungulinid because of its marked resemblance to the larvae of the Ripiphoridae, which were originally designated by that term. It is, however, essentially a planidium, and various authors have called attention to the similarity of its adaptive characters and habits to those of the planidia of the Eucharidae, Perilampidae, Cyrtidae, etc.

Pierce and other authors have described the triungulinids of a considerable number of species, and the characters available appear to be sufficient to permit of determinations of this instar to the family. Further study may reveal a basis for determination to lower groups.

In general, the triungulinids are fusiform in outline with the head and body segments heavily sclerotized, ranging in color from amber to shining black, the segmental bands terminating in pleural plates lateroventrally, the abdomen bearing one or more pairs of cerci or stylets on the terminal segments and a caudal sucker. After feeding has taken place, the bands become widely separated because of the

stretching of the thin intersegmental membranes and reveal the white color of the body contents. In size, the triungulinids are quite small, seldom exceeding 0.3 mm. in length, and many are only half that length. This is understandable in view of the large numbers produced by each female.

The head in most species is somewhat semicircular in outline, often slightly longer than wide, and occasionally is almost quadrangular. The eyes are usually large and situated slightly beneath the lateral margin. They consist of a group of three to five lenses, variously arranged, which are underlaid by masses of pigment. A few species apparently lack the lenses entirely. The antennae may be entirely absent, as in *Eoxenos laboulbenei*, or occasionally disk-like or slender and two- or three-jointed, as in *Callipharixenos muiri* Pierce and *Stichotrema dallatorreanum* Hof.

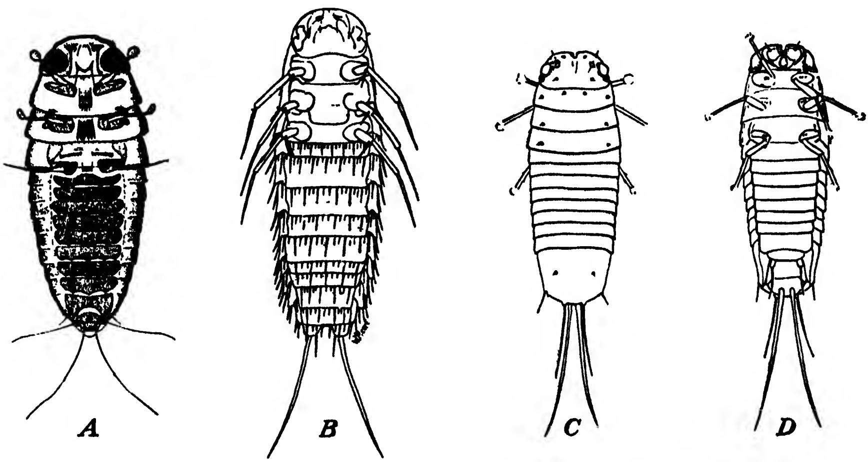


FIG. 218.—First-instar larvae of the Strepsiptera. *A*, *Corioxenos antestiae* Blair, ventral view (*from Kirkpatrick*, 1937); *B*, *Stylops californica* Pierce, ventral view; *C* and *D*, *Stichotrema dallatorreanum* Hof., dorsal and ventral views (*from Pierce*, 1918).

In many species, the mandibles are exceedingly minute and spine-like or entirely lacking, but in the last two species named they are rather large, curved, and directed backward. *E. laboulbenei* has the maxillae very long and spine-like.

The thoracic segments are longer than the abdominal segments following and are strongly arched. There is considerable variation in the 4-jointed legs of the various species, particularly in the tarsus. In *Stylops californica* Pierce (Fig. 218*B*), the tarsi are spine-like and equal in length to the tibiae, whereas in *C. muiri* they are only half as long as the tibiae and terminate in three filaments or claws. In the majority of species, however, the tarsi of the first two pairs of legs are in the form of large disk-like pulvilli, and those of the hind legs are slender and tapering. All three pairs of legs of *Stichotrema dallatorreanum* (Fig. 218*C*, *D*) are stated to have the pulvilli. The unguliform tarsus of the hind leg of *Xenos bohlsi* Hoff. is replaced by a ladle-like pad. The tarsi of all the legs of *Stylops swenki* are described as being acuminate in form and nearly half the length of the tibiae.

The abdomen consists of 10 segments of gradually decreasing width, though *Callipharixenos* is said to have only 7 segments. The first eight segments are short and of approximately equal length, whereas the terminal two are often considerably modified. In *Stichotrema dallatorreanum*, the ninth segment equals the preceding five in length, and the tenth is small and situated beneath the ninth. The last seg-

ment is frequently emarginate and bears two pronounced terminal tubercles from which the stylets arise. Only a single pair of caudal stylets is found in the majority of species, these being one-half to two-thirds the length of the body, though two pairs are mentioned for certain species of *Xenos*, *Elenchoides*, *Corioxenos*, *Belonogastechthrus*, and *Mecynocera* and three pairs for *Neocholax jacobsoni* Meig. If two pairs are present, the anterior pair is shorter and is usually borne on the ninth segment. The three pairs on *Neocholax* are all borne on the penultimate segment, and in *E. laboulbenei* the two pairs are both on the terminal segment.

The integumentary armature is almost entirely lacking in a great many species but some, such as *Stylops californica* (Fig. 218*B*), bear numerous spines in a transverse ring on the posterior margins of the abdominal segments. A few minute setae are found on the dorsum of the head and thorax. In *C. antestiae* (Fig. 218*A*), the thoracic segments bear heavy plate-like structures, with serrate posterior margins, ventrally between the legs.

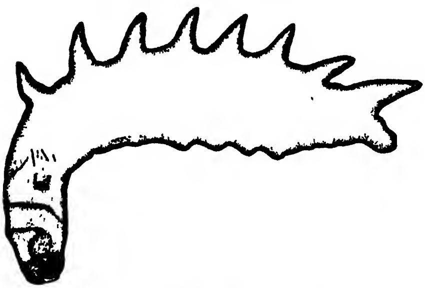


Fig. 219.—The seventh-instar female larva of *Corioxenos antestiae* Blair before extrusion of the cephalothorax from the body of the host. (*From Kirkpatrick*, 1937.)

The tracheal system has not been studied in any species, and in no instance has the triungulinid been found to bear spiracles.

The second-instar larva of *X. vesparum* is described by Nassanov as a simple apodous form, tapering toward both ends, with a thin integument and no fleshy protuberances or processes. Brues's description of that of *S. melittae* mentions a median row of 12 fleshy protuberances, considered to be locomotory in function, on the venter of the body. In *Corioxenos antestiae*, small paired protuberances representing the legs are present on the thoracic segments.

In the third instar of *Corioxenos*, the male still retains traces of the legs, but these are lacking in the female. The latter now shows the first indications of median dorsal protuberances on the body segments. The fourth instar is quite similar, with the leg rudiments conspicuous in the male, and the dorsal prominences of the female are distinct. The latter are conspicuous on the fifth instar of both sexes. In apparently all species, the sexes can be differentiated in the third instar by the presence, in the female, of two or three columns of massed cells extending the length of the abdomen on each side of the intestine.

The sixth-instar female larva shows the differentiation of the cephalothorax, which is as yet unsclerotized, with a pronounced constriction at its juncture with the abdomen, and is deflected ventrally. The spiracles of both sexes and the mouth parts of the female are sclerotized.

The seventh-instar larva of both sexes of *Corioxenos* retains the fleshy dorsal processes on the abdominal segments, though they are much larger in the female (Fig. 219). In the male, there are sclerotized bands on the cephalothorax, and after extrusion the entire structure in both sexes becomes heavily sclerotized and brown in color. The side in contact with the host body, which in this species is the venter, is appreciably flattened in the female. The cephalothorax of the male is almost quadrangular in form and larger than that of the female. This greater size of the male is also found in the species attacking Homoptera, as contrasted with the opposite condition in the species attacking Hymenoptera. The fleshy dorsal processes disappear as the body becomes distended with eggs. These processes are considered to serve principally to increase the absorptive area of the body, but they also function

in a limited way in locomotion. In all species, the cephalothorax becomes heavily sclerotized, the color being white at the time of extrusion but changing in a few hours to yellow, cinnamon, or brown. In certain species, the segmentation of the cephalothorax is indicated at the lateral margins, and in *Corioxenos* it is revealed by distinct lines in the male and definite constrictions in the female. Throughout the order, the exserted cephalothorax of the two sexes can be readily distinguished, that of the female being appreciably flattened dorsoventrally, whereas that of the male is more or less cylindrical, its depth very nearly equaling the width.

The Male Pupa.—The male pupa is distinctive in form and is found within the abdominal portion of the unbroken larval exuviae. According to Pierce, the seventh instar is really a pupa, which is enclosed by the sixth larval exuviae, and a second pupal instar then follows. After transformation, the adult male is consequently enveloped in three skins. In *Corioxenos*, the pupal skin is pushed downward to the posterior end of the puparium.

The Adult Female.—Because of the retention of the larval form by the adult females of the family, their persistence within the host body, and the peculiar development of the reproductive system, it seems desirable to give here a general description of that stage. It has been mentioned that in the apodous forms the seventh-instar female larva transforms directly into the adult without the intervention of a pupal stage. Much controversy arose among early entomologists as to the orientation of the body of the female, some claiming that the exserted portion was the head and others that it was the posterior portion of the abdomen. The latter appeared logical in view of the emergence of the triungulinids at that point. There was also considerable doubt as to the sides of the cephalothorax that were to be designated as dorsal and ventral. The true interpretation was arrived at only by an examination of the nervous system.

The adult female, as usually described, consists of the cephalothorax of the last larval instar plus the abdomen of the adult. Whether or not exuviation is complete is not known; if it does occur, the head and thorax of the adult female must be undifferentiated, with the cuticle thin, transparent, and following closely the inner surface of the cephalothorax. Certainly, the spiracles of the last larval instar, as well as other structures of the cephalothorax, serve the adult, also. The exuviae of the abdomen remains closely enveloping the adult except for a definite area ventrally which draws somewhat away from the body to form the brood chamber (Fig. 220*A*). According to Muir, the last larval exuviae of *Elenchoides perkinsi* is broken over the dorsum of the abdomen as a result of the great distention of the body of the female that accompanies egg production. According to Nassanov, the adult female of *S. melittae* is enveloped in two larval exuviae rather than only one.

In many species, the portion of the exuviae forming the brood chamber becomes considerably darkened, in contrast to the white of the remainder of the body. The brood chamber varies in width and length among the different species and extends to the posterior margin of the fourth segment in *Dacyrtocara undata* and to the eighth in *Xenos vesparum*, whereas in other species it is of intermediate length. This depends on the number and position of the genital pores. The chamber usually extends one, and occasionally two, segments beyond the last pore. The epithelium lining the ventral surface of the body and forming the dorsal wall of the brood chamber is appreciably modified, with the cells produced into spiny processes (Fig. 220*D*). This spinose surface is said to facilitate the escape of the triungulinids.

Westwood originally called attention to the existence of a cord or tube connecting the base of the abdomen to the integument of the host, and it was suggested that food is taken into the body by this means. Pierce observed the same feature in *Halictoxenos crawfordi* Pierce and in several Xenidae, but no definite information is available

regarding either its structure or function. Ulrich states that it is of host origin and that it serves as a means of attachment. It is quite possible that this structure represents an ingrowth of the integument, or rather a scab formation, analogous to the respiratory funnel formed about the posterior end of parasitic tachinid larvae which maintain, for respiratory purposes, a constant communication with the exterior through an aperture in the body wall of the host. The wound resulting from the extrusion of the cephalothorax is large, and, without complete healing, resulting in a close union of the intersegmental membrane with the "neck" of the parasite, the host would soon die from desiccation or disease.

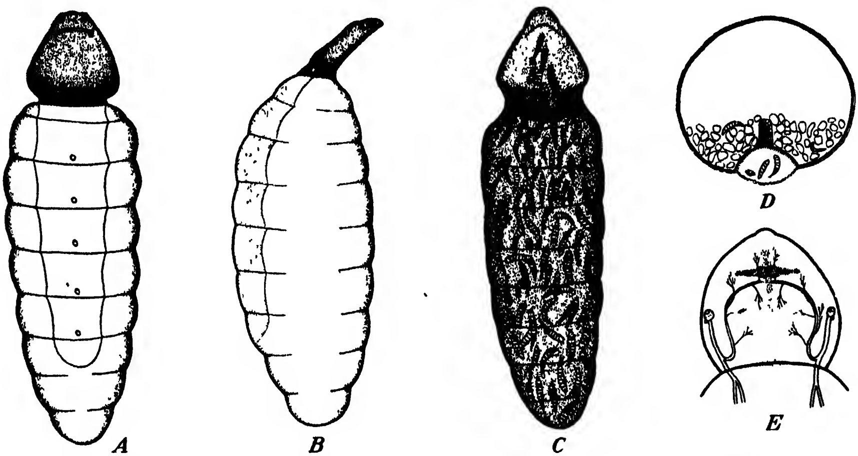


FIG. 220.—Adult females of the Strepsiptera, with details. *A*, *Stylops melittae* Kirby, showing the genital openings on the cephalothorax and the brood chamber; *B*, the same, lateral view; *C*, a gravid female of *Halictophagus curtisii* Dale, showing fully developed triungulinids distributed throughout the body; *D*, a diagrammatic cross section through the fourth abdominal segment of *S. melittae*, showing the outer portion of the genital canal and several triungulinids in the brood chamber; *E*, cephalothorax of *Xenos vesparum* Rossi, dorsal view, showing the single pair of spiracles, the anterior commissure and the longitudinal tracheal trunks, which divide in the first thoracic segment. (*Redrawn, after Nassanov*, 1892, '93.)

The characters that have been utilized thus far for describing the larviform females are as follows (Pierce, 1909, '18):

Measurements:

Head—width at emargination at base of mandibles in relation to thorax.
Cephalothorax—width at base of head, at spiracles, and at base; length from front edge of spiracle to apex of head and from base to apex of cephalothorax.
Mandibles—presence or absence, and form.
Spiracles—number, position, and form.
Genital pores—number and position.
Genital openings—number and form.

Distinct mandibles are present in the heads of the adult females of the Stylopidae, Xenidae, and Hylecthridae. In a few species, these are simple and small, but in the majority they bear a distinct tooth at the inner apical angle and may be widely separated. They are vestigial or absent in the Halictophagidae and Elenchidae.

These widely spaced thorn-like mandibles may be utilized by the mature larva in effecting the extrusion of the cephalothorax from the body.

The tracheal system of the mature larva usually comprises a pair of large spiracles on the cephalothorax, with branches extending throughout the body. In *X. vesparum* (Fig. 220*E*) and *S. melittae*, according to Nassanov, the two main anterior trunks are directed caudad from the spiracles; just before leaving the cephalothorax, each one gives off a branch that extends forward, and the two then unite to form a dorsal commissure. The main trunks divide immediately after entering the abdomen and reunite in the eighth segment, thus giving a dorsal and ventral trunk, with various branches, on each side of the body, and a posterior commissure. Smith and Hamm, however, mention only a single trunk on each side, with numerous ramifications, in *S. melittae.* According to Pierce, the paired lateral trunks are normal for the order. With few exceptions, the adult females have a single pair of rather large spiracles

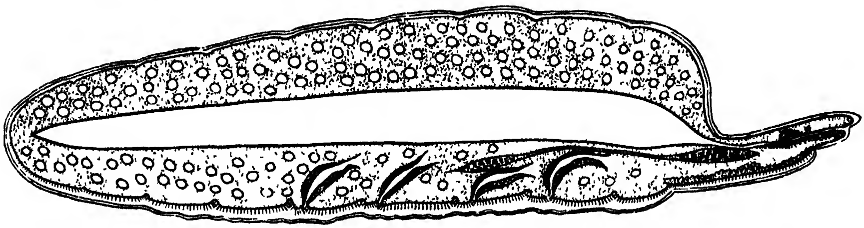


FIG. 221.—A longitudinal section of the adult female of *Xenos vesparum* Rossi, showing the spherical eggs lying free in the body cavity, the open genital canals leading from the body cavity to the ventral brood chamber, and the larval exuviae enveloping the entire body. (*Redrawn, after Nassanov*, 1892.)

situated at the lateral margins of the metathorax. *Callipharixenos muiri* and *Chrysocorixenos siamensis* Pierce have two pairs, and *D. undata* is distinguished by three pairs of small, slit-like spiracles at the margins of the abdominal brood chamber, in addition to the thoracic pair. Presumably, the metathoracic spiracles are closed until the extrusion of the cephalothorax from the body of the host. The exact stage in larval development at which the spiracles appear has not been determined in any instance, though Nassanov and others have implied that they occur in all instars after the first.

The reproductive system of the female is of remarkable form and not at all comparable with that found in any other insect. The eggs lie free in the body cavity, though Brues detected a rudimentary oviduct and vagina in *Xenos wheeleri.* On the median ventral line of the abdomen, there first appears a series of invaginations of the cuticle that develop into funnel-like structures, the inner ends of which become open about the time the larvae are mature. These are the genital duct or pores, through which fertilization takes place and the larvae later escape. These pores are usually found on the second and following abdominal segments, though in *Corioxenos antestiae* the first one is on the third segment. The number of pores is two in the case of *Dacyrtocara undata;* three in *Elenchinus japonicus* E. & H., *Elenchoides perkinsi* and *Crawfordia labiata* Ogl.; four in *X. bohlsi*, *X. vesparum*, (Fig. 221), *X. wheeleri*, *Tridactylophagus mysorensis*, and *Corioxenos antestiae;* and five in *Halictoxenos viridulae* Pierce, *Halictophagus curtisii* Dale, *Chrysocorixenos siamensis*, *Callipharixenos muiri*, and several species of *Stylops*. A very unusual arrangement of these pores is found in *Stichotrema dallatorreanum*, in which species they occur in three transverse rows of 12 to 14 each on the first or second abdominal segment. Hofeneder has erected the superfamily Stichotrematoidea on the basis of this character.

The genital opening usually occurs as a transverse crescentic slit ventrally at the juncture of the head and thorax; it is through this opening that fertilization takes place and the triungulinids later emerge. There is considerable variation in the form of this opening among the different species; it is almost semicircular in *Elenchoides* and *Elenchinus*. The opening is usually closed by a membrane, which is perforated at the time of mating. A striking departure in respect to the genital opening is found in *Corioxenos antestiae* in which, instead of being single and medially placed, it is paired, with one opening occurring at each side of the cephalothorax. This arrangement is said to be essential in order that mating may be accomplished, for the cephalothorax, except for one lateral margin, is covered by the wing of the host.

The free-living adult females of *Eoxenos* (Fig. 217*B*) and *Mengenilla* differ in many morphological characters from those which are permanently internal in habit. They are wingless and have primitive compound eyes, and the single genital opening occurs ventrally at the posterior margin of the seventh abdominal segment. In *Eoxenos*, the antennae are five-jointed and the legs have four-jointed tarsi terminating in a pair of claws, whereas in *Mengenilla* they are four- and three-jointed, respectively.

The reproductive system of *E. laboulbenei*, which has been studied by Parker and Smith, is quite different from that already described and approaches the type common to that of most other insects. The vagina is distinct and terminates anteriorly in the fifth abdominal segment, at which end it is apparently open. The eggs lie free in the body cavity, and some may even be contained in the head. There is no evidence of segmental genital pores on the median ventral line of the abdomen. Spiracles are present on the first six abdominal segments.

COLEOPTERA

The predaceous feeding habit is found to a greater or less extent in many families of this order, which probably contains the majority of all insects of predaceous habit. In the Adephaga, the species of the families Cicindelidae, Carabidae, Dytiscidae, and Gyrinidae are nearly all predaceous; they feed rather generally upon insects of suitable size occurring in the medium that they inhabit but attacking many other forms of small animal life, also. In the Polyphaga, the outstanding predaceous groups are the Silphoidea (Silphidae), Staphylinoidea (Staphylinidae, Histeridae), Cantharoidea (Lampyridae, Cleridae, Cantharidae), Mordelloidea (Meloidae), and the Cucujoidea (Coccinellidae). Although the great majority are rather general feeders, yet certain families are considerably restricted in their host preferences. The Silphidae commonly feed upon dipterous larvae present in decaying flesh, whereas most of the Lampyridae, in both the larval and adult stages, subsist mainly upon snails, earthworms, etc. The greater portion of the Meloidae are predaceous upon the eggs of Locustidae in the soil and the remainder develop in the cells of bees. The large family of coccinellid beetles, though containing some phytophagous forms, attacks principally the Aphididae, Coccidae, and Aleyrodidae. From the point of view of control of crop pests, the Coccinellidae and Carabidae are probably of greatest importance.

The parasitic mode of life is not nearly so common in the Coleoptera as in the Hymenoptera and Diptera, and only eight families are known to exhibit this relationship with the host. Possibly the entire small family Leptinidae exhibits a facultative parasitism, and in the Staphylinidae many species of the subfamily Aleocharinae (*Aleochara*, *Coprochara*, and *Baryodma*) are parasitic in dipterous puparia. In the Cleridae, a number of species of *Hydnocera* have been recorded as parasites, and some *Trichodes* apparently develop in the same way. The Ripiphoridae are entirely parasitic upon hymenopterous larvae and cockroaches. A few species of Colydiidae (*Bothrideres* and *Deretaphrus*) are apparently parasitic, and this is true, also, in *Catogenus* of the Passandridae. Certain species of Anthribidae of the genus *Brachytarsus* may be considered as parasitic, in one sense of the term, inasmuch as the larval food is strictly limited to the eggs beneath a single coccid host and the stimulus for oviposition by the female is provided by the scale itself rather than by the eggs. A few Coccinellidae, limited to those which attack the larger

monophlebine Coccidae, might also be considered as parasitic, in that the larva may, and often does, develop entirely at the expense of a single host individual.

Internal parasitism is exceedingly rare except in the Ripiphoridae, in which family it is normal for all species. Among the species attacking cockroaches the entire feeding period is passed internally, whereas in those attacking hymenopterous larvae the internal phase is limited to the latter portion of the first larval stage and the following stages are external. Information as to internal parasitism by the Colydiidae consists of isolated records of larvae taken from pupae of *Chrysobothris*, and the relationship has not been corroborated experimentally.

The parasitic species of the order, so far as known, show a considerable uniformity in habit and in the manner of development. Information on the early larval stages of species of this habit is very incomplete or entirely lacking for the Cleridae, Colydiidae, and Passandridae, the more or less complete details being at present available only for species of the families Staphylinidae, Ripiphoridae, and Meloidae. All of these deposit their eggs apart from the host stages upon which development is to take place, placing them in the soil, in host galleries, or on foliage or blossoms. The first-instar larvae of the parasitic Staphylinidae search out the dipterous puparia in the soil; those of the Ripiphoridae attacking cockroaches, and apparently a few of the Meloidae attacking bees, gain access to the host stages directly. The great majority of species of the latter two families that attack vespoid wasps and bees, respectively, appear to require the services of a carrier to transport them from the vicinity of hatching to the cell, and this role is usually filled by the female wasp or bee. Larval development among the parasitic species also reveals certain points in common that are not possessed by the predaceous forms. A marked hypermetamorphosis takes place during the course of larval development. The planidium type of first-instar larva is of common occurrence in the Ripiphoridae and Meloidae and in the parasitic representatives of several other families. The later larval instars assume a degenerate form in which the appendages are greatly reduced and the powers of locomotion are very limited or entirely lacking. The nonfeeding larval stages of the Meloidae have not been recognized in other parasitic groups of the order with the exception of the Drilidae.

Balduf (1935) has presented a comprehensive review of the biology and habits of the entomophagous Coleoptera, to which the reader is referred for a more complete account, particularly of the predaceous groups, than is given here. The illustrated synopsis of the larval forms of the order, by Böving and Craighead (1930 to 1931), deals with the specialized larvae of a number of species of parasitic and predaceous habit.

CICINDELIDAE

The tiger beetles, so-called because of the markings of the elytra in some species and the manner in which the adults attack their prey, are conspicuous also because of the metallic color of the elytra of many species and their extreme agility in running and flight. The great majority are terrestrial in habit, some are arboreal, and others semi-aquatic. All species, so far as known, are predaceous in both the adult and the larval stages, and the food consists of a wide variety of insects and other small animals. The very active winged adults obviously have a much greater choice of food than the larvae, which are dependent upon whatever may come within their limited reach. A few species are

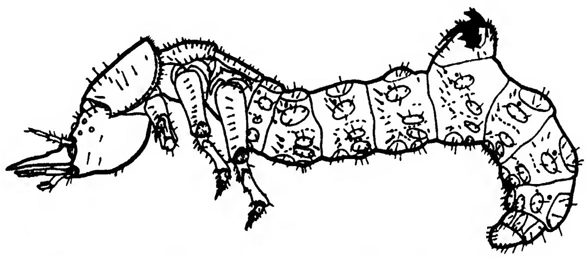


FIG. 222.—The larva of *Omus californicus* Esch. (*From Hamilton*, 1925.)

associated with termite nests, though their exact status is uncertain. Shelford (1909) and Hamilton (1925) present extensive biological data on many species, and Balduf (1935) gives an excellent summary of the habits of the family.

The terrestrial members of the family inhabit exposed situations such as paths, roadways, and sandy areas. In oviposition, the female excavates small cavities, less than ½ in. in depth, in the soil, and in these the translucent, ovate eggs are deposited singly. The larvae reveal a number of morphological modifications that fit them for an active predaceous life and for movement in the burrows that they inhabit. The head and pronotum are large and heavily chitinized, and the mandibles are exceedingly large and powerful and are bent somewhat upward, so that they serve for several purposes in addition to seizing and holding the prey. Ventrally, the head is markedly convex. The legs are equipped with long sharp claws, and these, in conjunction with the heavy, forwardly directed hooks on the dorsum of the fifth abdominal segment and with the distinctly S-shaped body, permit of ready movement in the burrow and serve to brace it in position in case of a struggle with a powerful victim.

The depth of the burrow is somewhat dependent upon the type of soil in which it is made; it also varies appreciably among species and

with the age of the individual larvae. Some species have been noted to make burrows in sand 1 to 2 m. in depth, though the majority do not exceed ½ m. The burrows are usually perpendicular with respect to the surrounding ground surface.

In waiting for its prey, the larva lies with its head at the entrance of the burrow, the claws and dorsal hooks well-embedded in the walls, and strikes out with an exceedingly rapid movement when an insect or other animal of suitable size comes within range.

The winter is passed most frequently in the larval stage, though a few species hibernate as adults at the bottom of the closed burrow. Just prior to pupation, the larva closes the entrance and forms a special pupation chamber either at the bottom of the burrow or at one side of the main shaft. The life cycle of the tropical species usually covers one year, whereas in colder regions this may be extended to three or four years.

The arboreal species of *Collyris* and *Tricondyla* occurring in Java differ from those inhabiting the soil mainly in the location of the burrow, which is formed in young twigs of plants. The initial entry hole through the bark and into the pith is made by the parent female with her ovipositor. This hole is plugged by the female after the egg is laid. The burrow is increased in size as the larva develops. Coffee trees are particularly susceptible to injury of this type, and ants that tend various scale insects, particularly *Pseudococcus* spp. and *Coccus viridis* L., are probably the principal food of the species that inhabit the twig burrows.

CARABIDAE

The ground beetles constituting this family are predominantly predaceous, the prey consisting mainly of insects but including also earthworms, snails, etc., though a few species are questionably phytophagous and others at times partake of plant food in addition to the normal insect diet. Several species are associated with ants and termites. The insect feeders attack lepidopterous larvae and naked pupae more generally than they do the immature stages of other orders, though a number of species are recorded as feeding extensively upon scarabaeid grubs in the soil. They undoubtedly destroy a wide variety of soft-bodied insects. As in several other predominantly predaceous families of Coleoptera, occasional species have developed the habit of obligatory external parasitism, with a resulting degeneration in the larval instars following the first molt.

As is implied by the common name given to this group, the adults are predominantly ground dwellers, and they carry on their activities mainly at night. They may be found in various protected locations, such as under stones and debris and the loose bark of trees, or they may

inhabit distinct burrows. Many other species, particularly of the genera *Calosoma* and *Lebia*, are to a certain extent arboreal in habit, and they may be frequently found attacking foliage-feeding insects in trees.

In many cases, the feeding habits of the adult beetles vary considerably from those of the larvae, which is understandable in view of their greater size and mobility. Thus, a number of species of *Carabus*, *Craspedonotus*, and other genera have been recorded as attacking and feeding upon adult beetles, snails, etc. *Calosoma inquisitor* L. of Europe is particularly abundant in areas bearing broad-leaved trees, upon the foliage of which it searches for caterpillars. The variety of food consumed by the adults is appreciably greater than that consumed by the larvae, partly owing to their greater agility, enabling them to capture insects that can escape from the larvae. Feeding may be very rapid, consisting of the biting or tearing away of portions of the tissue of the victim after the integument has been broken, or it may be solely by the ingestion of liquid materials, resulting from preoral digestion of the host tissues, in addition to the body fluid. The tendency toward feeding upon plant materials has attracted considerable attention. Forbes (1883) analyzed the stomach contents of 175 specimens, representing 18 genera, in which it was found that vegetable food, consisting largely of pollen and cryptogamic plants, comprised 43 per cent of the total. Several species of *Harpalus* and *Pterostichus* have been recorded as pests of strawberry fruits, though it is believed, in some instances at least, that such feeding is primarily the result of a need for water. Other species are known to partake of water regularly in addition to the moisture derived from their normal foods.

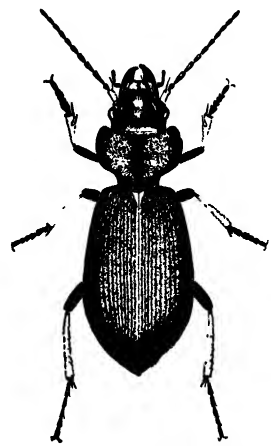


FIG. 223.—The adult female of *Craspedonotus tibialis* Schaum. (*From Clausen et al.*, 1927.)

In several species, it has been established that the newly hatched larva does not feed for several days after hatching, for its needs are provided by yolk, derived from the egg, which is contained in the digestive tract. Preoral digestion occurs among some larvae, as is true also among the adults, whereas others ingest the tissues directly. The injection of an intestinal secretion associated with preoral digestion has a paralyzing effect upon the host, which is of importance where there is a marked disparity in size between the predator and host. The quantity of food consumed by a carabid larva is often very great when compared with its own size. Thus Burgess (1911, '17), and Burgess and Collins (1915), in their studies upon *C. sycophanta*, found that each larva consumed an

average of 41 sixth-instar gypsy-moth caterpillars during its feeding period, which covered an average of 14 days. Pairs of adults were found to destroy 100 to 460 sixth-instar larvae between the time of emergence of the beetles in the spring and the cessation of their feeding in midsummer.

Irrespective of the feeding habit of the larvae, whether on the surface of the ground or in trees or shrubbery, all the predaceous species of Carabidae pupate in cells in the soil, often at a considerable depth. Thus *C. sycophanta* under normal field conditions forms its pupal chamber 10 to 12.5 cm. beneath the surface, but at other times it penetrates much deeper. This habit ensures a considerable degree of uniformity in temperature and humidity, which is essential for pupae not adapted to a wide range in these conditions. The few instances of pupation aboveground occur among the parasitic species, such as *Brachinus*, in which it takes place in the pupal cell of the host.

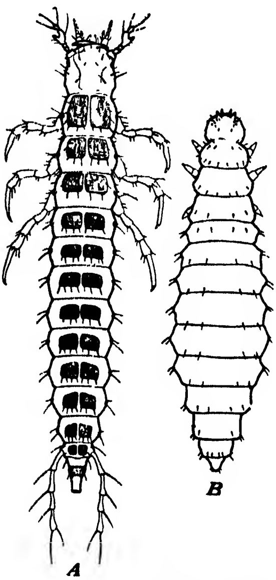


FIG. 224.—*A*, the first-instar larva of *Lebia scapularis* Fourc.; *B*, the second-instar larva of same. (*From Silvestri*, 1904.)

The occurrence of the parasitic mode of development in the Carabidae has been established in several genera that are widely separated taxonomically. This relationship with the host was first recorded in *Brachinus janthinipennis* Dej. by Wickham (1894) and was corroborated by Dimmock and Knab (1904). The larvae were found in the pupal cells of *Dineutes assimilis* Aubé and showed the modifications in form, such as reduction of the legs to a nonfunctional condition, that are usually associated with the parasitic mode of life.

The most detailed account of the parasitic development of a member of the family is that of *Lebia scapularis* Fourc. by Silvestri (1904). The adult beetles feed upon all immature stages of the elm leaf-beetle, *Galerucella luteola* Mull., whereas the larvae are restricted to attack upon the pupae. The first-instar larva (Fig. 224*A*) does not differ appreciably from others of the family; it is rather elongate, with 13 body segments, each of which bears sclerotized plates, and the legs are long and well-developed. The caudal cerci are four-jointed. After locating the host pupae in the soil, the young larva feeds voraciously through a large puncture which it makes in the integument and in which the head is embedded. Following the first molt, a grub-like form is assumed (Fig. 224*B*) in which the segmental plates and the caudal cerci are lacking, and the legs are reduced to mere short conical processes. This

is followed by the prepupal and pupal stages, in both of which the meso- and metathoracic segments are considerably produced laterally. Before larval feeding is complete, the spinning of the cocoon takes place. This cocoon is composed of a mass of interwoven strands cemented together and is lemon-yellow or brown in color. During the process of spinning, the remains of the host pupa may be drawn into the cocoon and enclosed within it. Two generations are produced each year, and the winter is passed in the adult stage in sheltered places.

Observations have been made by Salt (1928) upon the habits of *Pelecium sulcatum* Guer., one of an aberrant genus of Carabidae. Several

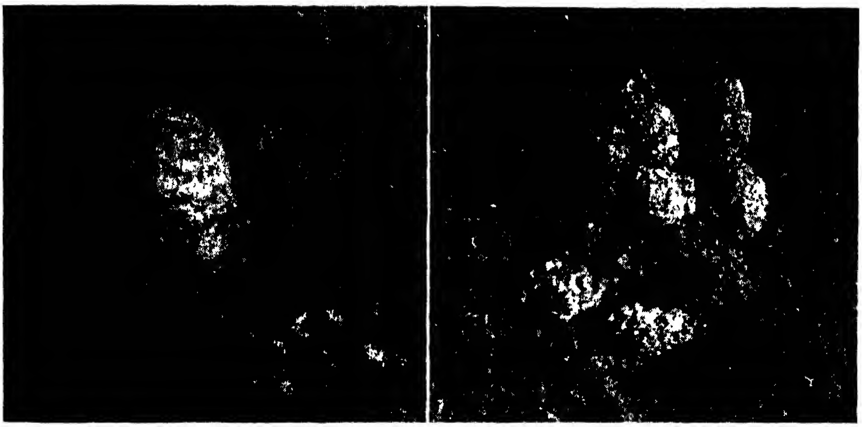


FIG. 225.—The mud egg cells of *Brachinus cyanipennis* Say. At left is a group of cells near a *Gyrinus* cocoon upon a stone and, at right, a group of egg cells, much enlarged. (*Photographs by J. L. King and H. B. Kirk.*)

larvae were found upon various hosts, including beetle pupae and millepedes. Development was rapid and was apparently completed upon a single host individual, so that in its essential points the mode of life is identical with that of *Lebia,* though no distinctive second-instar larva was found and no cocoon is spun.

Blair (1927) gives an interesting account of the habits of *Arsinoë grandis* Per., which appears to represent a transitional phase between predatism and parasitism. The larvae were found attacking those of the lichen-feeding tenebrionid beetle, *Catamerus revoili* Fairm., in Nyasaland. A number of the larvae of the latter were found to bear those of *Arsinoë* attached by the mandibles to the dorsum of the abdomen. Feeding takes place in this position until the death of the host, whereupon the larva releases its hold and searches out another host. The younger larvae may feed for as long as two weeks before bringing about the death of the host, whereas the later instars do so in one or two days. Pupation takes place in the soil. The duration of larval life was not determined

with exactness, though it very evidently is rather long, for some individuals that were collected did not enter the soil for pupation until several months later. From this it would appear that a number of host individuals are essential to bring the beetle larva to maturity.

In general, it may be stated that the eggs of the Carabidae are deposited in the immediate vicinity of the hosts upon which the larvae

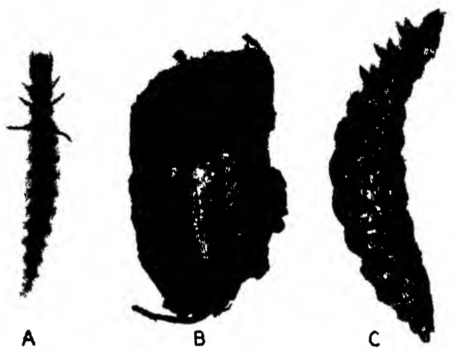


FIG. 226.—The larvae of *Brachinus cyanipennis* Say. *A*, the first-instar larvae; *B*, a second-instar larva feeding upon a *Gyrinus* pupa in its cell; *C*, the third-instar larva. (*Photographs by J. L. King and H. B. Kirk.*)

are to feed, though not closely associated therewith. So far as known, the habit of the parasitic species in this respect does not differ appreciably from that of the predaceous forms. The great majority of species of Carabidae deposit their eggs singly in small holes made in the soil with the ovipositor. *Pterostichus multipunctatus* Dej. is reported to place a cluster of eggs in the soil chamber and then to stand guard over them during the incubation period and for a time after hatching.

King (1919) has shown that several species of *Brachinus*, *Galerita*, and *Chlaenius* place the eggs singly in mud cells which they build upon plant stems, leaves, stones, etc., a habit first recorded by C. V. Riley in 1884. The form and composition of the cells, as well as their location, are distinctive for the various genera. The cells of *Brachinus* are crescentic or triangular and are found in groups of 3 to 10 on the undersides of stones, twigs, and plant stems, whereas those of *Galerita* are triangular or purse-shaped, with a finely granular surface, and are formed on the undersides of smooth leaves. In *C. impunctifrons* Say, they are oblong and smoothly convex and are likewise placed on the undersides of smooth leaves, whereas those of *C. aestivus* Say are found upon dead twigs, plant stems, the bark of trees, etc. In forming the cell, the mud pellet is first collected about the tip of the abdomen of the female beetle, and the walls are built up on the stone or other surface in the form of a

mold about the caudal segments. The cover is formed from the mud carried upon the dorsum of these segments.

The most elaborate provision for egg-laying is that of *Craspedonotus tibialis* Schaum. (Clausen *et al.*, 1927) which inhabits sand-dune areas in certain sections of Japan. The female beetle digs a burrow 25 to 45 cm. in depth, inclined at an angle of 45 deg., in embankments, and the eggs are placed singly in small chambers branching off from the main burrow. Apparently, the entire egg-laying period of the female is passed in this burrow, except for periodic forays for food.

The life cycles of the Carabidae are exceedingly variable, ranging from several months in the case of *Lebia grandis* to several years. The great majority probably have an annual cycle, with the winter passed in the adult stage, though in many species the adult beetles may live for several years. Burgess has made extended observations on the habits of *Calosoma sycophanta* and finds that the adults normally pass through two winters, and often three or four, though none was found to deposit eggs for more than two seasons. The duration of life of the males is virtually the same as that of the females. In this and most other species, the adult stage is reached late in the season, and oviposition does not begin until the following spring. Some individuals in fact do not oviposit until the second season. A large series of *C. sycophanta* produced an average of 128.5 eggs per female, with a maximum of 653. The average for the family, however, is believed to be considerably below these figures.

DYTISCIDAE

The diving beetles comprising this family are largely, if not entirely, predaceous in both the larval and the adult stages. Their food consists of a wide range of animal life, including practically all forms which live in the aquatic habitat of the beetles and which are of a size that can be overcome. Some of the larger species even prey upon the smaller fish, at times causing considerable loss in fish ponds and hatcheries. Snails, tadpoles, earthworms, and even small frogs are also attacked. The majority of species, however, subsist upon the immature stages of other aquatic insects, principally the Odonata, Ephemerida, and Hemiptera. The larvae and adults have in general the same food source, though the latter, being more agile, have a greater choice. In feeding, the beetles bite away portions of the victim and swallow them bit by bit, whereas the larvae partake only of liquid food, a habit that is made possible by the presence of a narrow canal or channel extending from near the tip to the base on the inner margin of each mandible. Like many other Coleoptera, the majority of larvae of this family inject a digestive secretion into the body of the host, which to a considerable extent

liquefies the solid tissues. Balduf (1935) has presented a detailed review of the biology and habits of the family.

The adults of the family are not limited to an aquatic life, for some species are able to use the legs for running and the majority are capable of extended flight. However, the body has been appreciably modified for aquatic life, as is revealed by a closer union of the body parts, a pronounced streamlining of the body, the flattening of the legs, and the development of fringes of heavy hairs on the inner margins of the tarsi. The incompleteness of this adaptation to aquatic life by the family is revealed by the pupation habit. After the completion of feeding, the mature larvae leave the water and form their pupation cells in mud or soil, under stones or other objects, or among rubbish. In each case, a distinct cell is formed, which is spherical, oval, or pyriform and which in the larger species may be 5 cm. or more in diameter.

There is an appreciable difference in the manner of locomotion of the larvae of the various species. Species of several genera move about solely by crawling over the bottom or over rocks and vegetation. Other species swim only occasionally, but many are very active swimmers and thus come to the surface and capture their prey. The bodies of the latter group are lighter than the surrounding water, which enables them to come to the surface with ease. The legs of some species are equipped with fringes of hairs, which greatly facilitate swimming.

In oviposition, the eggs of some species are deposited in masses in mud or debris at the water's edge, singly on the surface of floating leaves, or in individual incisions in submerged plant tissue. The latter habit is common to the majority of species. Some damage may at times be inflicted on ornamental aquatic vegetation through excessive oviposition, resulting in wilting and death of leaves and stems.

Usually, a single generation is produced each year, though the adults may live for several years. The duration of the life cycle is directly dependent upon the temperature of the surrounding water, and incubation of the eggs may consequently be prolonged from one week or less to several months. The great majority of species pass the winter in the adult stage in the water, becoming active and ovipositing early in the spring. Others hibernate as larvae, and the adults appear in midsummer.

An interesting feature of the larvae of the Dytiscidae is their ability to regenerate lost parts. Lost legs and antennae appear to be only partly replaced at the following molts but are fully regenerated in the pupal stage. The replacement is much more complete when the parts are lost by first-instar larvae than when they are lost by the following instars.

HYGROBIIDAE

This small family, which is closely related to the Dytiscidae, is aquatic in habit and lives in ponds rather than in streams. The food preferences and general habits are little known except for the account of *Hygrobia hermani* F. (*Pelobius tardus* Hbst.) published by Balfour-Browne (1922*a*). The adults are found in the mud at the bottom of ponds, and the females deposit their eggs in rows on the submerged stems of aquatic plants. The larvae feed upon worms and the immature stages of the less active aquatic insects. The mature larva leaves the water for pupation and forms a cell in the soil 5 cm. or more beneath the surface. A single generation is produced each year, and the winter is passed in the adult stage in the mud at the bottom of the pond.

GYRINIDAE

The whirligig beetles comprising this family are found to inhabit standing or slowly flowing water. The adults are quite gregarious in habit, and the schools of gyrating beetles are most noticeable during the latter part of the season. The adults, like those of related families, are capable of extended flight as well as of swimming and diving. Their bodies are likewise markedly modified in form, producing a rigidity in structure and a distinctly streamlined effect. The last two pairs of legs are short and much flattened and bear an outer fringe of flattened hairs, which appreciably increases the area and consequently gives greater efficiency in swimming. In swimming and diving, the beetles carry a supply of air in a space beneath the elytra.

The adults subsist largely if not entirely upon animal food though they are generally considered to be scavengers rather than predators. They feed upon various insects that fall into the water. The larvae, on the other hand, are strictly predaceous and feed upon the body fluids of almost any form of animal life available in the aquatic environment which they inhabit and that is of suitable size to be captured.

The eggs are deposited in masses, often arranged in rows, upon the surface of submerged foliage. Incubation is complete in one to two weeks.

The species of which the life histories have been studied leave the water for pupation. The pupal case, which may be built up from a wide variety of materials, is constructed by the mature larva either upon the ground or on plant stems or leaves above the water surface.

So far as known, the species occurring in temperate regions have a single generation each year and pass the winter in the adult stage. Some species bury themselves in mud during this period, whereas others remain upon the water or cling to vegetation beneath the surface.

HYDROPHILIDAE

There is a considerably greater variety in habits among the species of this family than in the strictly aquatic groups already discussed. The majority of species are aquatic in habit, but a number of the subfamily Sphaeridiinae are known to be terrestrial in all stages, living in moist soil or associated with animal excrement. The adults are commonly known as water scavenger beetles. An extended account of the habits of the family is given by Balduf.

The aquatic species are most frequently found in pools and ponds having an extensive growth of vegetation, though they also frequent streams. The adult beetles feed principally as scavengers, consuming decaying animal matter and also living or dead plant tissue. A great many species subsist very largely upon algae and other lower forms of plant life. With few exceptions, the larvae of the family are predaceous, feeding upon various Entomostraca, worms, snails, insect larvae, and pupae, and even small fish, crayfish, and tadpoles. They not only consume the body fluids but may swallow bits of solid matter, also.

A few species of the genus *Dactylosternum* are known to be predaceous upon crop pests. *D. hydrophiloides* M'Leay, *D. dytiscoides* F., and *D. cycloides* Knisch. attack larvae of the sugarcane beetle borer, *Rhabdocnemis obscura* Boids., in the Philippine Islands and were imported into Hawaii from 1925 to 1926 for use against this pest. More recently, the first-named species and *D. abdominale* F. were imported into Jamaica in the attempt to control the banana borer, *Cosmopolites sordida* Germ.

The oviposition habit of the aquatic members of the family is of particular interest because of the silken case within which the eggs of many species are contained. Several of the more primitive subfamilies deposit their eggs singly, with little or no covering. In several genera, the cases are attached to the body of the parent by silken strands, whereas in others they are enclosed in a folded leaf, placed on foliage beneath the water surface, or float free upon the water.

The larvae of the great majority of aquatic species are incapable of swimming; they move about by crawling along the bottom or upon vegetation and may be found only partly submerged. With a few exceptions, the larvae of the family construct their pupal cases out of water. These are found near the water line in mud, under various objects, or on plants above ground. *Enochrus* is reported to form its case from floating strands of *Spirogyra.*

So far as known, one or two generations are produced each year, depending upon the species concerned, and the winter is passed in the adult stage.

SILPHIDAE

The carrion beetles are, as the names implies, usually found associated with decaying animal matter, which is generally presumed to be the principal food. Investigations in recent years, however, have shown a considerable range in food preferences of both the adult beetles and the larvae. A few species are found associated with ants, others develop in decaying fungi, many feed upon a combination of animal matter and insect larvae, and a small number of species are apparently obligatory predators upon other insects. Occasional species subsist largely, if not entirely, upon snails.

Among the Silphidae that have a mixed diet, the insect prey consists largely of dipterous larvae, principally those of blowflies, that are present in the decaying flesh. In addition, the beetles will attack many other insects that frequent carcasses.

The adults of *Xylodrepa quadripunctata* L. of Europe are arboreal in habit and are apparently restricted to a predatory role, the favored food consisting largely of smooth-skinned caterpillars, sawfly larvae, aphids, and other foliage-inhabiting insects. Caterpillars with only a light covering of hairs may also be attacked. The larvae, however, feed only upon the ground. An effort was made at one time to introduce this species into the United States for the control of the gypsy moth.

STAPHYLINIDAE

This family, comprising the rove beetles, is represented by a large number of species. The adult beetles are readily recognized by their relatively slender bodies and very short elytra and by the habit of elevating the abdomen when disturbed. There is a wide range in food habits. Though the great majority of species are probably scavengers, yet a considerable number are predaceous upon other insects and a few are true parasites. Extended reviews of the host preferences and habits of the family are given by Mank (1923), Voris (1934), and Balduf (1935).

The large number of myrmecophilous Staphylinidae range in habit from true guests to active predators, and in the latter case both larvae and adults prey upon all stages of the host. In some groups, such as *Lomechusa*, the adult beetles have special glands that secrete a substance much favored by the ants, and the larvae, which prey upon the younger stages of the ants, are carefully tended during their development. A number of species of Aleocharinae are found associated with termites, though none is known to feed upon them.

From the point of view of natural control, we are particularly concerned with the free-living predaceous and parasitic forms rather than with those which are a part of a complex social organization. A great

number of species, in both the adult and larval stages, are predaceous upon other insects, and especially upon dipterous larvae in decaying animal bodies, refuse, or in the soil. The genus *Nudobius* is known to be predaceous upon various insects found beneath the bark of trees infested with bark beetles, and the adults of several species of *Paederus* are recorded as important enemies of the eggs and larvae of lepidopterous and other foliage-feeding pests. In Formosa, it is reported that 65 per cent of the larvae of the rice borer, *Schoenobius incertellus* Wlk., are thus attacked. In Egypt, *P. fuscipes* Curt. is stated to be the most important of the natural enemies of the cotton worm, *Prodenia litura F.*, and the field population may reach 50,000 per acre. *Somatium oviformis* Casey is a well-known predator upon red spiders and mites on citrus trees in California, and others of that genus have the same food source.

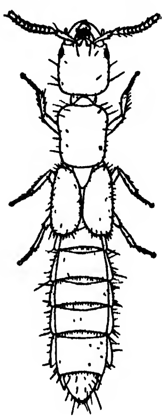


FIG. 227.—An adult of *Nudobius pugetanus* Casey (*From Struble,* 1930.)

Philonthus aeneus Rossi and *Creophilus erythrocephalus* F. have been imported into Hawaii, the former from Germany and the latter from Australia, for the control of the horn fly. The latter species is known to have become established.

The parasitic species of the Staphylinidae are contained in the subfamily Aleocharinae, the best known being of the genera *Coprochara, Aleochara,* and *Baryodma.* The larvae of these are obligate external parasites upon the pupae of Diptera, but within the puparium. Wadsworth (1915) has presented an extended account of *C. bilineata* Gyll., a parasite of the pupae of the cabbage maggot, *Hylemya brassicae* Bouché. It is the dominant parasite of this pest and destroys up to 35 per cent of the pupae. The female deposits her eggs in the soil near the roots of infested cabbage plants. These eggs are elliptical in form, measure 0.38 by 0.32 mm., and have a thin, transparent chorion. Those recently deposited are greenish-white in color, becoming darker as incubation progresses, and hatching takes place in 10 to 12 days.

The first-instar larva is not readily distinguishable from those of the predaceous and scavenging species, which is understandable in view of the active life that it leads before reaching the host. It must first search about in the soil to a depth of 2 to 15 cm. until a *Hylemya* puparium is encountered, and it is then under the necessity of penetrating the more or less hardened shell. The puncture is sealed after entry has been effected.

The body of the newly hatched larva is about 1.5 mm. in length, rather slender, and distinctly segmented, with 10 abdominal segments, of which the last two are darker in color and taper to a rounded point.

The head is large and likewise darker in color than the body, and the antennae are three-jointed and well-developed. The legs are normal for the family. The caudal cerci are shorter than those of most other species and are borne on short cylindrical processes dorsolaterally at the posterior margin of the penultimate segment.

After entering the host puparium, the larva begins feeding through a minute puncture made in the delicate cuticle of the pupa. The feeding position is changed frequently but is apparently limited to the anterior dorsal region. When fully fed, the body of the parasite is considerably enlarged, the transparent intersegmental membranes being greatly stretched, and the average length is about 2.0 mm.

The second-instar larva is markedly different from the first, being quite degenerate as a result of the adoption of a parasitic mode of life. The body is glistening white, with the cuticle very lightly sclerotized, and the setae and cerci are absent. The legs are rudimentary and indistinctly segmented and lack the large terminal claw. Each of the last two thoracic and the first eight abdominal segments has a single pair of fleshy prominences at the dorsolateral margins. Feeding by this stage is extensive, and very little movement takes place.

The third-instar larva is identical in all general characters with the second but is, of course, considerably larger. As in the preceding instar, there are nine pairs of spiracles, situated between the first and second thoracic segments and on the first eight abdominal segments, respectively. In *Aleochara* and other genera that pupate outside the host puparium, the segmental tubercles or prominences mentioned above are lacking. During the feeding period, no excrementary matter is voided with the exception of occasional minute drops of a clear fluid, and the meconium is cast by the mature larva. The host pupa is completely consumed, and the puparium becomes opaque because of the meconial covering on the inner surface. The pupal form is normal for the family.

Under summer conditions, the feeding period is complete in five to six days after the first molt and is followed by a quiescent stage of 12 to 18 days prior to the appearance of the pupa. The pupal stage also requires 12 to 18 days, at the completion of which the adult beetle gnaws its way out of the puparium. The adults are very active and feed extensively upon the cabbage maggots that they encounter. There are presumably two generations each year, corresponding to the cycle of the host, and the winter season is passed as a first-instar larva within the host puparium. The first brood of adults appears in May and June and the second in August and September.

Although the great majority of parasitic members of the family attack puparia occurring on or in the soil, yet occasional species find

their hosts upon or in plants. *Maseochara valida* Lec. was found by Coquillett (1891) to develop in the puparia of a syrphid fly, *Copestylum marginatum* Say, which develops in the semiliquid material in the decaying leaves of cactus.

An extended study is presented by Kemner (1926) upon *Aleochara curtula* Goeze, parasitic in the puparia of *Lucilia*, etc. Its habits are in general quite similar to those of *C. bilineata*, except that the third-

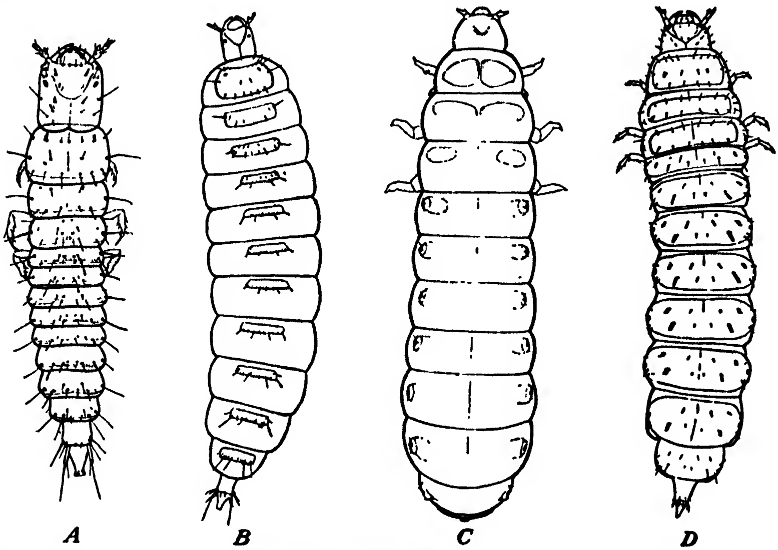


FIG. 228.—The larvae of *Aleochara curtula* Goeze. *A* and *B*, the newly hatched and fully fed first-instar larvae; *C* and *D*, second- and third-instar larvae. (*From Kemner*, 1926.)

instar larva assumes an active and more normal form, with the legs sufficiently large and well-developed for locomotion, and that it emerges from the puparium for pupation in a cell in the soil. This habit is found in the genera *Aleochara*, *Baryodma*, *Polychara*, and *Maseochara*, whereas the more degenerate form, which pupates within the host puparium, is found in *Coprochara* and *Polystoma*.

B. bimaculata Grav. is recorded by Lindquist (1936) to develop in the puparia of *Sarcophaga* and *Cryptolucilia* in Texas. The planidium enters the puparium in the same manner as already described for *Coprochara*, and emergence of the adult occurs about 20 days later. The field parasitization of these hosts is approximately 25 per cent.

Observations have been recorded upon various other species of parasitic Staphylinidae, and it appears that the adults of these species are also quite important as enemies of the same pests, as they are predaceous upon both the larvae and pupae.

Quayle (1913) records the habits of *Somatium oviformis*, a minute species that, so far as known, feeds mainly upon red mites. This is true of both the adult and larval stages. The eggs are light-orange in color and are deposited singly upon the undersides of the infested leaves. The larvae consume an average of 20 mites per day, and the adult beetles about half that number.

Mank has given an account of the habits and descriptions of the immature forms of a series of species predaceous upon dipterous larvae occurring in decaying vegetable matter. These species belong to the well known genus *Philonthus* and related groups. Both adults and larvae feed extensively upon maggots found in the medium in which they live. The life cycles of the different species were found to be relatively short, the cycle from egg to adult being completed in one month or less.

The larvae of the predaceous species are very active and aggressive. The body is elongate in form, and individuals may be readily distinguished from carabid larvae by the prominent two-jointed caudal stylets and by the single claw of the tarsi. They also generally lack the distinct heavily sclerotized segmental plates often seen in the Carabidae, though these plates are present in *Tachinus*. The character found to be most reliable in distinguishing larvae of the family is the so-called "upper lip," which varies in the number and size of the teeth borne at the anterior margin. The abdomen terminates in a relatively large "pseudopod" or "pusher," which is consistently utilized in locomotion.

The pupae present few distinguishing features, and the principal character utilized in separating species is the fringe of hairs at the anterior margin of the thorax and those at the lateral margin of the abdomen. In *Tachinus*, the integument of the pupa is soft, and the body is completely covered with a soft material which becomes silvery in appearance.

HISTERIDAE

Both the adults and larvae of this family are commonly found associated with decaying animal or vegetable matter, which led to the earlier assumption that their role was principally scavengerous. A number of species are myrmecophilous in habit. Evidence is accumulating, however, to show that many species are, in reality, predaceous upon various insects. Coleopterous and dipterous larvae constitute the bulk of their prey. A few species live in the open and attack immature stages of Chrysomelidae and Lepidoptera. The larvae of species of a considerable number of genera are limited in their host preferences to the immature stages of wood-inhabiting Coleoptera, principally of the Scolytidae and other soft-bodied insects found in or beneath bark (Balduf, 1935). Struble (1930) records the adults of *Plegaderus nitidus* Horn as being predaceous upon the eggs of *Dendroctonus*, and those of *Platysoma*

punctigerum Lec. feed upon a variety of insects found under the bark. The latter species places its eggs along the sides of the bark-beetle egg galleries. These hatch in 10 to 14 days, and larval development is complete in four to six weeks and is followed by a pupal stage of 10 to 14 days. There are two generations each year, the overwintering brood of adults ovipositing in May and the second brood emerging from July onwards. The larvae are active searchers and feed upon many insects in addition to *Dendroctonus* larvae.

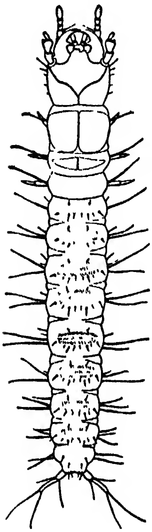


FIG. 229.—The mature larva of *Platysoma punctigerum* Lec. (*From Struble*, 1930.)

Plaesius javanus Er., in both the larval and adult stages, is predaceous upon the larvae and pupae of the banana borer, *Cosmopolites sordida* Germ., in Java. It has been introduced into Fiji for the control of this pest, and satisfactory results have been secured in those sections where the crop is grown under uncultivated conditions. Attempts have also been made to establish it in Australia, Hawaii, Formosa, Uganda, and several West Indian islands, but these have resulted successfully only in Australia. The life cycle of this predator is long, covering a period of nearly one year, and the adult beetles are very long-lived, even when deprived of food. *Hister bimaculatus* L. was introduced into Hawaii from Germany in 1909 as an enemy of the horn fly.

LAMPYRIDAE

This family comprises the bulk of the well-known glowworms or fireflies, which are found throughout the world, and are conspicuous because of the luminescence produced by certain organs. All stages are luminous, even the eggs being faintly so owing to the material with which they are coated at the time of deposition. A few species are diurnal in habit and have these organs only slightly developed or entirely lacking. In most species, the female is wingless and somewhat larviform and of considerably greater size than the male. A few species are said to be plant feeders in the adult stage (Williams, 1917), though the great majority, both as adults and larvae, appear to limit their feeding mainly to snails, with some evidence that earthworms and cutworms may also constitute a portion of the diet. The amount of food consumed by the larvae is very much greater than that consumed by the adults; many of the latter apparently do not feed at all. The larvae evidently inject a powerful toxic agent into the body of the snail host, for death takes place very quickly after it is bitten, though the mechanical injury is comparatively slight.

Several Asiatic species are known to be aquatic in habit, the larvae of some living in clear flowing streams whereas others inhabit standing water such as is found in rice fields. The food consists largely, if not entirely, of aquatic snails.

The larval life of most of the known terrestrial species appears to cover two years, whereas the aquatic forms have an annual cycle. Hibernation is in the larval stage in a soil chamber upon or beneath the surface. Pupation usually takes place in a soil cell, beneath rubbish or on the surface in moist situations. Information on the biology of several of the more common North American species is presented by Hess (1920).

Hutson and Austin (1924) have studied the life history and habits of *Lamprophorus tenebrosus* Wlk. which is predaceous upon the terrestrial African or Kalutara snail, *Achatina fulica* Fer., a serious truck-crop pest in Ceylon. In Japan, *Luciola cruciata* Motsch. is a well-known enemy of aquatic snails (Okada, 1928; Kanda, 1933). In many tropical countries, the control of these snails is important, not because they inflict direct damage in any way but because they serve as intermediate hosts of human-disease organisms.

Lampyris noctiluca L. has recently been imported into New Zealand from England for the control of *Helix adspersa* Mull.

DRILIDAE

So far as known, the food of the larvae of this family consists solely of snails; no information is available regarding the food habits of the adult beetles. Certain species that have been extensively studied show a remarkable sexual dimorphism, the males being winged and the females apterous and larviform.

The eggs are deposited in large masses in shallow burrows in the soil. The females are capable of producing 300 to 500 eggs, and, in some cases at least, the entire quota is deposited in a single day. There is a considerable range in the exceptionally long periods of incubation recorded for the different species, which vary from six weeks to about three months.

The first-instar larva is similar in general form to the larvae of other families of the order. It is very active and carries on an extended search for snails upon which to feed. When one is found, a firm hold on the shell is taken by the anal sucker, and it is then dragged to some sheltered position, after which entry into the shell is effected. Considerable difficulty is often experienced in passing the barrier provided by the operculum. Feeding is gradual as compared with that of lampyrid larvae on the same hosts, and death of the snail may not take place for many days after entry is effected. It is thus evident that no digestive juices or toxic fluids are introduced into the body during this early feeding period. The body of the mature larva is greatly distorted and twisted,

owing to confinement in a cavity of spiral form. In *Drilus flavescens* Rossi, which has been studied in detail by Crawshay (1903) and other authors, there appears a distinctive resting stage, induced by adverse conditions such as food shortage and adverse climatic conditions, that is comparable with the coarctate stage in the Meloidae. The integument of this instar is thin, nearly white, and largely bare, and the head and body appendages are small and rudimentary. Return to the active feeding stage is accomplished when favorable conditions again prevail. Pupation takes place within the host shell.

The cycle from egg to adult covers a period of three or four years; during this time, two to four snails may be eaten each season. The total number of molts has not been determined. Normally, the larva molts after completion of feeding on each host and immediately before it abandons the shell. The adult beetles appear in late spring and early summer.

Extended accounts of the life histories and habits of *D. mauritanicus* Lucas and *Malacogaster passerinii* Bassi have been presented by Cros (1926, '30).

PHENGODIDAE

Very little is known regarding the habits of the family, though it is stated that the American species of *Phengodes* prey upon myriapods. In some species, both the larvae and the adults have light-producing organs.

CANTHARIDAE

This family comprises the so-called soldier beetles, many of which are predaceous in habit, though others are phytophagous. The adults of many species of *Podabrus* and *Cantharis* are known to feed extensively upon Aphididae, and the larvae of *C. rustica* Fall. have been recorded as feeding upon grasshopper eggs and lepidopterous and coleopterous larvae. Those of *Chauliognathus marginalis* are said often to enter the burrows of *Heliothis obsoleta* F. in corn and destroy them, and *C. pennsylvanicus* Deg. is reported to destroy many adult *Diabrotica* during the latter part of the season when they were inactive. The latter species is stated by C. V. Riley to be predaceous in the egg masses of locusts. Although the adults and larvae are probably mainly predaceous, yet they also feed to a varying extent upon a wide assortment of plant materials, including plant seeds, roots, etc.

The eggs are deposited in masses in the soil or beneath various objects and hatch in about one week. The newly hatched individuals, of some species, at least, are embryonic in form, having the appendages feebly developed, and are termed "prolarvae." The intestine is filled with yolk, which is the sole food until the first molt has taken place. The

number of larval instars is uncertain. Pupation takes place in cells in the soil.

One or two generations are produced each year, and the winter is passed in the advanced larval stage in sheltered places. The adult beetles are found mainly during early summer.

Cantharis rufa var. *lituratus* Fall. is an omnivorous feeder, but at times it derives the bulk of its food from syrphid larvae, *Platycheirus albumanus* F., which enter the soil for hibernation and pupation (Payne, 1916). Experiments indicate that the larvae feed readily upon seeds of cereal crops but that vegetables are attacked only incidentally and after the initial break in the skin has been brought about by other agencies.

MALACHIIDAE

A considerable range is revealed in the food preferences of the members of this family. According to Xambeau (1908), a number of species are predaceous upon wood-boring larvae, whereas others subsist upon soft-bodied insects and other small animals living in protected places. Some species are considered to be scavengers, feeding upon dead insects.

In the genus *Collops*, there are a considerable number of species that prey upon a variety of insect pests. *C. quadrimaculatus* F. feeds upon leaf hoppers and has been recorded as an extensive predator upon the eggs of the chinch bug, though it does not attack the nymphs or adults. *C. bipunctatus* Say preys upon larvae of the alfalfa weevil, *Hypera postica* Gyll., and on the eggs of the grain bug, *Chlorochroa sayi* Stal.; *C. vittatus* Say feeds very extensively upon both living and dead larvae and pupae of the alfalfa caterpillar, *Eurymus eurytheme* Boisd. *C. bipunctatus* is considered to be one of the most effective of the natural enemies of the grain bug.

CLERIDAE

The adults of this family are termed checkered beetles because of the color pattern on the dorsum of the body. With few exceptions, the species are predaceous in both the larval and the adult stages. They show an exceptional consistency in host preferences, the majority confining themselves to the Scolytoidea and other wood-boring or -inhabiting Coleoptera. They rank among the most effective natural checks upon these forest pests. *Thaneroclerus girodi* Chevr. is recorded by Runner (1919) as the most important of the natural enemies of the cigarette beetle, *Lasioderma serricorne* F., in the United States. The adults prey upon the adult beetles and the larvae upon the eggs and larvae in the burrows. Of particular importance because of their entomophagous feeding habit are a number of species of the genera *Thanasimus*, *Enoclerus*, *Tillus*, etc. *Trogodendron fasiculatum* Schreib., of Australia, is stated

to prey upon the pupae of wood-boring Lepidoptera. *Cymatodera undulata* Say is recorded by Balduf (1926*a*) as a predator on the larvae of a cynipoid wasp, *Disholcaspis mamma* Walsh, and other larvae inhabiting the galls that it produces. Several species are predaceous in the egg pods of Locustidae. The genus *Necrobia* departs from the general food habit of the family, and the various species subsist largely as scavengers, only occasionally partaking of living insect food. Beeson (1926) has made observations upon the habits of a large number of predaceous species associated with bark and wood borers in India. For a detailed

FIG. 230.—An adult of *Thanasimus formicarius* L. feeding upon a bark beetle and, at right, a mature larva of same. (*From Hopkins*, 1899.)

account of the food habits of the family, the reader is referred to the recent publication by Balduf (1935).

Callimerus arcufer Chapin has been studied in some detail by Tothill *et al.* (1930) as an enemy of the coconut moth in Malaya, and an attempt was made to introduce it into Fiji for the control of a related coconut moth, *Levuana iridescens* B.B. It is not restricted to these hosts but feeds quite generally upon soft-bodied insects found upon the trees. The eggs, which measure 1.6 by 0.4 mm., are thickest in the middle region, slightly curved, and yellow in color and are deposited beneath the host pupae. A maximum of 203 eggs was secured from a single female, with the average daily rate of deposition not exceeding 1, though at times up to 11 have been secured in one day. The larvae feed by preference upon the pupae, whereas the adults prey most extensively upon the larvae. There are three larval instars, though in some individuals the third is omitted. Pupation takes place usually, though not always, within a cocoon. The cycle from egg to adult requires a mini-

mum period of about five weeks, of which incubation of the egg covers 6 days and the larval feeding period about 19 days. The preoviposition period is 16 days or longer. Several generations are consequently produced each year.

Tarsostenus univittatus Rossi is predaceous, in both its larval and adult stages, upon powder-post beetles of the genera *Lyctus* and *Xylobiops* occurring in seasoned wood products. According to St. George (1924), the female inserts the extended ovipositor into the entrance gallery of the host and deposits one or several eggs therein. The eggs are very similar to those of the host, being elongate and cylindrical and with the anterior end drawn out into a slender stalk, which is about one-seventh the length of the main body.

Observations upon the habits of several species that attack primary and secondary bark borers have been recorded by Böving and Champlain (1920). The eggs are usually placed in the host entrance gallery or in cracks or crevices in the bark. The life cycle is usually correlated with that of the host, and a two-year cycle is indicated in some species. Because of the feeding of the larvae upon the immature stages of the host, it is necessary that the cycle shall approximately parallel that of the latter, for the stages suitable for attack are available for only a relatively short period of time. Species attacking a two-brooded host are themselves likely to have two generations each year.

The place of pupation is variable, some species utilizing the host gallery or pupal cell, whereas others form a cell in the soil at the base of the tree. In *Enoclerus sphegeus* F. and others of the genus, this cell is lined with a foam-like oral exudation. Some species of the family consistently pupate without forming a cocoon or cell. The hibernation habit is not uniform, as larvae, prepupae, pupae, and adults of a few species may be found during the winter, whereas other species may be represented by larvae or pupae only. The adults are present in the field during midsummer and may persist for several months.

Linsley (1936) discusses the habits of *Aulicus terrestris* Linsley as a predator of the lubber grasshopper, *Esselenia vanduzeei* Hebard, and of various lepidopterous larvae in California. The eggs are apparently laid singly under stones or in the soil in the immediate vicinity of the grasshopper egg masses. The larvae are very active and search about in the soil for their food, which seems to be limited to this single source. The life cycle coincides with that of the host, and the adult beetles appear in the late spring at the time the adult grasshoppers are active. The adults, however, do not prey upon any stage of the grasshoppers but subsist instead upon various naked lepidopterous larvae, particularly of the Noctuidae, found in or on the soil. This habit is largely confined to the females; the males quite consistently refuse such food.

Although the great majority of species of the family are predaceous in habit, yet a few develop, at least at times, as external parasites. These species are found principally in the genus *Hydnocera*. *H. verticalis* Say has been reared on several occasions from the cocoons of *Apanteles*. *H. pubescens* Lec. appears to be parasitic upon the larva of the cotton-boll weevil, *Anthonomus grandis* Boh., in its cell in the boll, and the parasite finally spins its cocoon and pupates in the host cell.

Sabrosky (1934) reared an adult of *Isohydnocera curtipennis* Newm. from a goldenrod gall (produced by a larva of *Gnorismoschema*), and an examination of the contents of the gall revealed the empty shell of the lepidopterous pupa, within which the cast skin of the beetle larva was found. Development was undoubtedly at the expense of a single host, but whether internal, as asserted by the author, or external is uncertain. Clancy's (mss.) observations upon *Hydnocera* spp. as enemies of codling-moth larvae in their cocoons indicate that, although the larvae are generally predaceous, yet true parasitic development is possible.

Several species of *Trichodes* (Cros, 1908, '11) that develop upon the larvae of various bees are somewhat on the border line between parasitism and predatism. Some reach maturity upon a single host; others move from cell to cell, devouring several larvae, and they may also consume such of the host food material as may be present. It is still uncertain whether the eggs are laid directly in the cell or nest; they may be deposited elsewhere and the host searched out by the young larva. The adults of some species feed principally upon pollen. Several species are recorded as attacking the larvae of honeybees in the hive, and the genus appears to be limited to hosts of this type. The general habits appear to be very similar to those of the Meloidae that develop in the cells of bees.

MORDELLIDAE

Several authors have asserted that certain species of this family are predaceous upon the larvae of stem- and wood-boring insects, but present-day workers do not concur in this conclusion.

Hill (1922) found larvae of *Mordellistena erythroderes* Hill in termite nests and asserts that they are predaceous upon these insects. Balduf considers that the form of the larvae in this family is not such as to adapt them to the aggressive mode of life required of a predator.

RIPIPHORIDAE

This family, which comprises only a few hundred species, is cosmopolitan in distribution and is of particular interest from several points of view. The adult beetles are rather striking in appearance with

the body markedly streamlined, the antennae of the males pectinate, and the color pattern of many species quite variable. The females of *Macrosaigon pusillum* Gerst. may be entirely red or black, or the thorax may be of one color and the elytra and abdomen of the other. The anomalous genus *Rhizostylops* described by Silvestri (1905) has certain characters and habits that seem to place it as an intermediate form between the Ripiphoridae and the Strepsiptera, and the adult females bear a marked resemblance to those of the genera *Mengenilla* and *Eoxenos* of the latter order. The adult females of *Rhizostylops* (Fig. 232) as well as those of several species of *Ripidius* are apterous, degenerate, and distinctly larviform.

All species, so far as known, are parasitic in habit and pass at least a portion of the larval period internally in the body of the host, an adaptation virtually unknown elsewhere in the order. This developmental habit is accompanied by a hypermetamorphosis somewhat comparable with that occurring in the Meloidae and certain parasitic Staphylinidae.

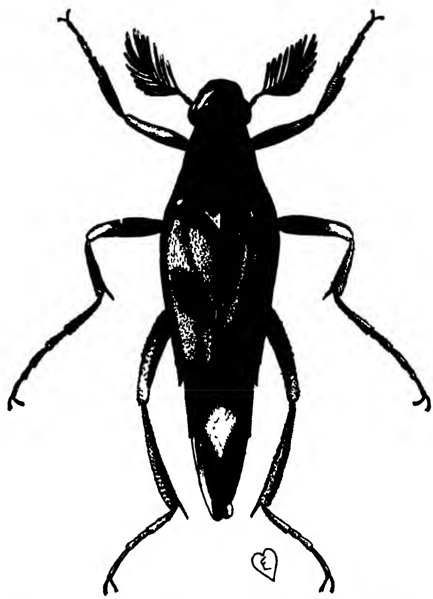


Fig. 231.—The adult female of *Macrosaigon pectinatus* F. (*From Davis*, 1919.)

The host preferences have been determined for only a relatively few species of the family. The majority appear to attack hymenopterous larvae of the families Vespidae, Andrenidae, Scoliidae, and Tiphiidae, and those most frequently encountered belong to the genera *Metoecus*, *Ripiphorus*, and *Macrosaigon*. Rather extensive parasitization of scoliid and tiphiid larvae in the cocoons has been noted in several instances. In *Tiphia pullivora* A. & J. of India, 28.4 per cent of the field-collected cocoons yielded *Macrosaigon pusillum* adults. In general, it may be considered that all representatives of the family developing upon Hymenoptera are harmful rather than beneficial. The host preferences and habits of *Rhizostylops* are unknown.

BIOLOGY AND HABITS

The species of *Ripidius* of which the habits are known depart from the normal for the family both in host preferences and in relationships.

R. pectinicornis Thbg., originally described in 1808, was recorded as a parasite of *Blatella germanica* L. under the name of *Symbius blattarum* Sund. by Sundervall in 1831. The mature larvae were found in the bodies of cockroaches on shipboard, and adult females were seen to deposit their eggs promiscuously. More recently, Stamm (1935, '36) has extended our knowledge of the habits and larval forms of this very interesting species. Schultze has recorded the rearing of *R. scutellaris* Hell. from Blattidae in the Philippine Islands, and *R. boissyi* Abeille of Europe is parasitic in the nymphs of *Ectobia.* The entire genus appears to be restricted in its host preferences to the Blattidae. It is further distinguished in habit from those developing upon hymenopterous larvae in passing the entire larval period within the host. *R. pectinicornis* is gregarious, one to five developing in each host, whereas those upon Hymenoptera appear to be consistently solitary.

Perhaps the most extensive observations have been made upon *Metoecus paradoxus* L. which is commonly found in Europe as a parasite of the larvae of *Vespa* spp. Westwood recognized the parasitic relationship as early as 1864, and Chapman (1870, '91, '97) first considered the species to be a commensal in the nest. Murray (1870*a*, *b*) agreed with the conclusions of Westwood. Rouget (1873) secured oviposition in the laboratory and surmised that under field conditions the eggs are laid on blossoms, foliage, etc., and that the young larvae are then carried to the nest by the *Vespa* adults. Chapman later found the much distended first-instar larvae, ten times their original length, within the bodies of the host larvae, just beneath the skin of the fourth or fifth segment. Only a portion of the first stage is passed internally, and the second-instar larva is found as a collar encircling the neck of the host.

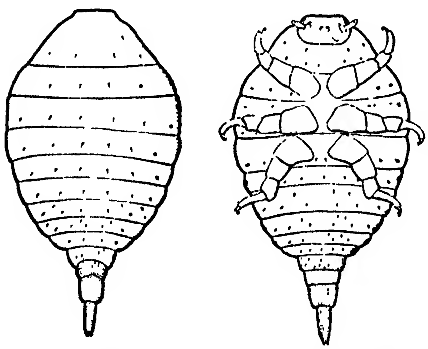


Fig. 232.—The adult female of *Rhizostylops inquirendus* Silv., dorsal and ventral views. (*From Silvestri*, 1905.)

The reproductive capacity of the members of the family is relatively high, as is to be expected in view of the high mortality that is inevitable in the first larval stage. Chobaut (1891) mentions that the female of *Macrosaigon flabellatum* F. deposits about 500 eggs, and Silvestri records approximately 3,000 for *R. inquirendus* Silv. These are usually laid in clusters, rather than singly. The place of oviposition is quite variable. *M. flabellatum* deposits its eggs in clusters in the soil and covers them lightly with earth. According to Jarvis (1922), *M. cucullatum*

Macl. places the eggs close together among the hairs on the undersides of the leaves of *Ficus* and *Urenia*. One hundred or more were found on a single leaf, covering an area of about 9 or 10 sq. cm. *Metoecus paradoxus* deposits them in crevices in decaying wood. *Ripiphorus subdipterus* Bosc. was observed by Chobaut (1906) to oviposit in the blossoms of *Eryngium*, and *R. solidaginis* Pierce (1904) does so in the green buds of goldenrod, *Solidago rigida*. The limited information on the oviposition habits of the family indicates numerous adaptations correlated with the location of the host stages and with the habits of the host adults in case the latter serve as carriers of the triungulinids. In no instance thus far observed have the eggs been placed upon or in close proximity to the host stages upon which development of the larva is to take place.

The manner in which the triungulinids gain access to the host is of particular interest, involving as it does transportation by some agency from the vicinity of hatching to the host larvae in their cells. The evidence on this point is fragmentary, and the interpretation of the known facts by various authors is at times contradictory. It is believed that the triungulinids themselves do not undertake an active search for either the host stages or the carrier but instead that they take up a position favorable to contact with a carrier and then await its coming. According to Chobaut, those of *M. flabellatum* attach themselves to the *Odynerus* adults and are thus carried to the nest. Pierce expresses the opinion that the triungulinids of *R. solidaginis* are carried by the *Ripiphorus* adults themselves, which are said to hibernate in the holes of *Epinomia*, its host. This explanation is offered in view of the occurrence of the triungulinids upon opening buds of *Solidago*, a plant that is not frequented by *Epinomia* adults. It should be noted, however, that numbers of them were found upon the bodies of bees of various genera living in the *Epinomia* community. The triungulinids of *R. subdipterus* are found on *Eryngium* blossoms and presumably attach themselves to *Halictus* adults which frequent this plant.

The habits of *M. cucullatum*, parasitic upon the larvae of *Campsomeris* spp. in Australia, are of particular interest. These wasps are external parasites of scarabaeid grubs in the soil. The triungulinids of *Macrosaigon* are found on the foliage of certain trees and the problem of reaching the host larvae in the soil, which are themselves parasitic and consequently receive no attention from the parent females, is more complex than that confronting the species mentioned above. Though no direct observations were made in the field, yet laboratory tests indicated that the triungulinids probably attach themselves to the *Campsomeris* females and are thus carried into the soil at the time the latter oviposit and that at this time they transfer to the scarabaeid grub and await the hatching of the *Campsomeris* egg and the subsequent development of the

larva. One triungulinid was noted to remain motionless upon an egg on a paralyzed grub for three days; during this time, it made no effort to pierce the chorion. Though development of this species is completed only on the mature larva in the cocoon, yet it is probable that the triungulinid attaches itself to the partly grown larva, or enters its body, prior to the formation of the cocoon.

There is as yet no evidence to indicate that the triungulinids of any species are able to effect parasitization of scoliid or tiphiid larvae after the cocoon has been spun.

Among the scoliid and tiphiid hosts of various species of this family, it is quite evident that, if the triungulinids of the parasite are carried

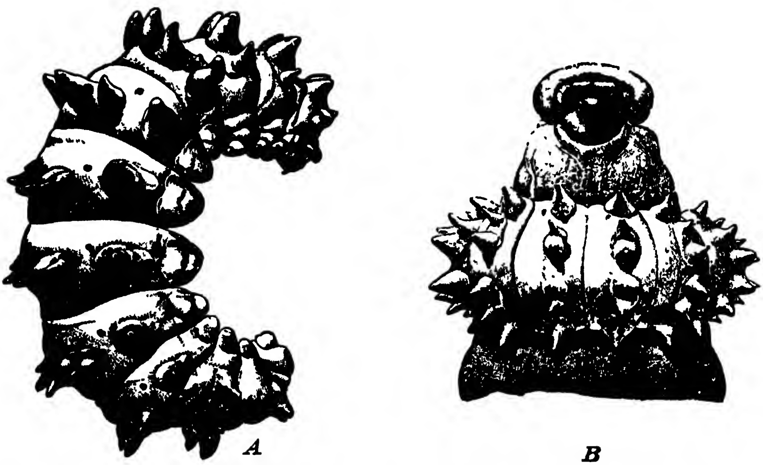


FIG. 233.—*Macrosaigon flabellatum* F. *A*, probably the last instar, lateral view, showing the conspicuous segmental tubercles; *B*, the normal external feeding position of the second and following instars upon the larva of *Rhynchium oculatum* Spin. (*From Grandi*, 1937.)

into the soil by the females at the time of oviposition, the extent of parasitization of the different species will vary greatly in the same locality, owing to the diverse feeding habits of these adults. Scoliid females feed principally at blossoms, whereas the spring species of Tiphiidae subsist almost exclusively upon insect honeydew and the summer and autumn species mainly upon the secretions from various nectar glands of plants. The relatively high mortality of *Tiphia pullivora* previously referred to is possibly linked to a more general tendency to feed at blossoms than is exhibited by other species prevalent in the field at the same season.

The simplest parasitic relationship in the family appears to exist in respect to the *Ripidius* species attacking the nymphs and adults of cockroaches. In this genus the eggs are apparently laid indiscriminately in crevices, etc., and the triungulinids attach themselves directly to pass-

ing hosts and enter the body for development, thus eliminating the need for a carrier.

The triungulinids of all species are equipped with a caudal sucker and one or two pairs of cerci of varying length by means of which they are able to assume an erect position, with the legs entirely free, while waiting to attach themselves to passing insects or other objects. They are presumed also to have the jumping habit common to larvae of this type.

The free-living phase of larval life may extend over a considerable period, during which, presumably, no food is taken. Pierce, however, believes that the triungulinids of *Ripiphorus solidaginis* feed upon the plant tissues or sap of *Solidago* soon after hatching. He bases this conclusion on two points: (1) that they are of considerably greater size than the egg; and (2) that they are found only on *Solidago*, which is not frequented by the host bees. It is assumed that this plant is utilized, in preference to others, in order to fulfill these food requirements. A transitory plant-feeding habit such as this is not in accord with the habits of larvae of this type, and the evidence presented does not definitely establish its occurrence. The increase in size that was noted may possibly have resulted from the imbibing of moisture from the leaf surface.

With the exception of *Ripidius pectinicornis* and others of that genus that pass the entire larval feeding period within the cockroach host, all the known species develop externally, having an internal phase only in the first stage. In some cases, this internal period of life is of short duration; but, in the case of *M. flabellatum*, entry into the *Odynerus* larva is effected during the late summer, and the parasite larva does not emerge for external feeding until the following June. The developmental cycle and larval habits are thus strikingly comparable to those of certain Perilampidae, particularly the species of hyperparasitic habit. Normally, the host larva is not killed until it has completed feeding and is preparing for pupation. The cells containing parasitized *Vespa* larvae and those of other host groups of similar habit as well are consequently closed in the normal way, and, in the case of the Scoliidae and Tiphiidae, the cocoons are spun before death.

The transition from the internal to the external feeding phase has been observed only in *Metoecus paradoxus* and *Macrosaigon flabellatum* (Grandi, 1937). In the latter species, the greatly distended triungulinid, which is several hundred times as large by volume as when newly hatched (Fig. 234*B* to *D*), emerges through a puncture in the third thoracic segment of the host, immediately casts its exuviae, which remains in the puncture, and then takes up the feeding position, in which it is found as a collar about the first or second thoracic segment (Fig. 233*B*). The triungulinid increases in length from 0.5 mm. at hatching to 2.5 mm.

just prior to the first molt. The host larva is eventually completely consumed.

The Life Cycle.—The majority of species apparently have a single generation each year, and this is closely correlated with the cycle of the host. According to Pierce, *Ripiphorus solidaginis* passes the winter in the adult stage and deposits its eggs early in the spring, and the adult stage is again attained in August. *Metoecus paradoxus*, on the contrary, deposits its eggs in the late autumn, and the fully developed embryo persists in the egg until spring. *Macrosaigon flabellatum* oviposits in the late summer, and the winter period is passed as a first-instar larva with the body of the *Odynerus* larva. *M. pusillum* probably has the same hibernation habit, for the adults emerge from the *Tiphia* cocoons during July. Barber[1] (1939), in discussing the observations of J. C. Bridwell upon *Ripiphorus* sp., parasitic upon *Augochlora pura* Say., mentions that the triungulinids are found attached to the hairs of hibernating fertilized female hosts. They pass the winter in this way, on the hibernating female bee, and transfer to her brood cells when these are formed in the spring. *R. solidaginis* is said to have two generations each year; *Ripidius pectinicornis*, which develops in cockroaches in the tropics, probably has a short cycle, with a number of generations annually.

The incubation period has been determined only for *M. flabellatum* and *M. cucullatum;* in these species, it is 17 and 7½ days, respectively. The larval feeding period of *Metoecus paradoxus* is stated to cover only 12 to 14 days.

IMMATURE STAGES

The eggs of the various species are relatively minute, ranging from 0.3 mm. in length in *M. flabellatum* to 0.7 by 0.15 mm. in *Rhizostylops inquirendus*. They are usually broader at one end, white, and in *Metoecus paradoxus*, at least, covered with a mucilaginous material.

The triungulinid first-instar larvae are of the planidium type, with the body smoothly tapered and the segments each bearing a heavily sclerotized band, with pleural plates, and separated by thin and very elastic intersegmental membranes, which are visible only after the commencement of feeding. The body color is blackish, owing to the heavily indurated segmental plates. The thoracic segments are large and broad, and the abdominal segments, which apparently range in number from 8 to 10, are of diminishing length. The head (Fig. 235) is somewhat triangular in form and heavily sclerotized and bears several ocelli, placed close together, at each side. The antennae are usually two-jointed, the second terminating in a long hair-like process which is considered by some authors to be a segment. The mandibles are heavy, simple, and sharply curved. The legs are long and slender, and the tibiae usually terminate in large leaf-like pulvilli. The body segments bear a variable number of integumentary setae and spines. In the majority of species, the two

[1] This author cites authority for the spelling of *Ripidius* and *Ripiphorus* in place of *Rhipidius* and *Rhipiphorus*.

caudal segments each bear a pair of cerci of varying length, and the abdomen terminates in a suctorial disk.

The characters of the triungulinid which show marked variation between species are: the antennae, the claws or pulvilli of the legs, the setae and conical spines on the body segments, and the caudal cerci. In most species, the antennae are two-jointed, the first often bearing a spine or branch near the distal end, though that of *Macrosaigon tricuspidata* is stated to be three-jointed. The large leaf-like pulvillus which is borne at the end of the tibia, in lieu of the tarsus, is replaced in *R. inquirendus* by a pair of minute claws, whereas in *Ripidius denisi* (Chobaut, 1919) the claws are present and also a small pulvillus. In *M. flabellatum*, pleural plates are present on the second and third thoracic and the first seven abdominal segments (Grandi, 1937). Perhaps the most conspicuous specific character is the number and arrangement of the spines and

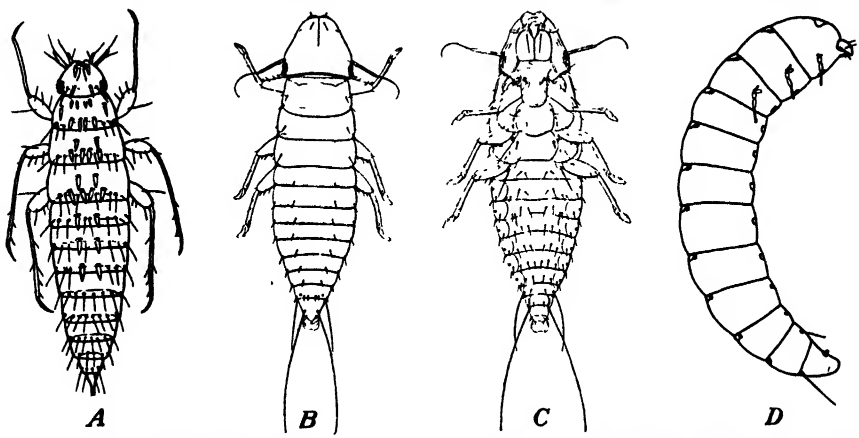


FIG. 234.—First-instar larvae of the Ripiphoridae. *A*, *Ripidius denisi* Chob. (*from Chobaut*, 1919); *B* and *C*, *Macrosaigon flabellatum* F., dorsal and ventral views, before feeding; *D*, the same, at the completion of the endoparasitic phase, immediately before the first molt, showing the extreme distention of the body and the wide separation of the segmental plates (*from Grandi*, 1937.)

setae upon the different body segments. A number of species, including *M. tricuspidata*, *M. flabellatum* (Fig. 234*B*, *C*), and *Ripiphorus solidaginis*, apparently have only a single seta at each lateral margin of the segments, and *Metoecus paradoxus* has a row of small setae dorsally and ventrally on each segment. *Ripidius denisi* and *Rhizostylops inquirendus* are distinguished by long setae at the posterior margins of the segments and heavy conical spines on the head and thorax, a pair of these occurring also on each of the first three abdominal segments in the first-named species. With respect to the caudal cerci, *Ripiphorus solidaginis* has only two very short pairs, whereas *Ripidius denisi* has one pair, these being only slightly longer than one or two segments. *M. paradoxus* and *Macrosaigon cucullatum* have a single long pair, also, but these are equal to the body in length. Other species have two pairs of unequal length; those on the last segment are longest and equal or exceed the body length in *M. tricuspidata* and *M. flabellatum*. In the latter species, the first pair occurs on the ventral plate of the penultimate segment, and the second pair is on the dorsal plate of the last segment.

The tracheal system has been examined and described only for *Rhizostylops inquirendus* and *M. flabellatum*. In the former species, spiracles occur only on the last two abdominal segments, and transverse commissures occur at the caudal end of

the body and in the second and third thoracic segments, whereas there are nine pairs in the case of *M. flabellatum*, these being situated on the pleural plates of the mesothorax and the first seven abdominal segments and at the lateral margins of the dorsal plate of the eighth segment.

Virtually nothing is known of the second-instar larva of any species. Stamm mentions it in the case of *Ripidius pectinicornis* and states that it is quite similar to the mature form. It is to be expected that all the distinguishing characters of the triungulinid would be lost at the first molt; and the second instar, being strictly a

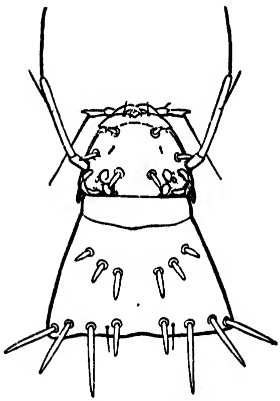


FIG. 235.—The head and first thoracic segment, dorsal view, of the first-instar larva of *Rhizostylops inquirendus* Silv. (*From Silvestri*, 1905.)

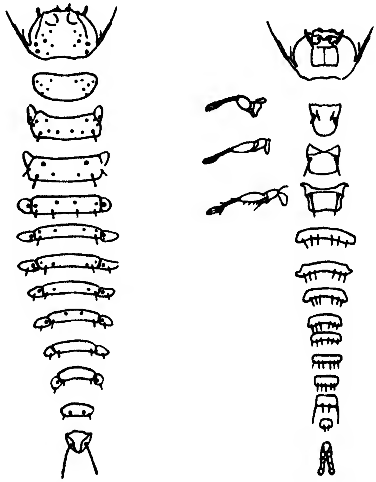


FIG. 236.—The exuviae of the first-instar larva of *Metoecus paradoxus* L., showing the plates of the dorsum and venter. (*From Chapman*, 1870.)

feeding form, is grub-like. What is presumably the second instar of *Metoecus paradoxus* is figured by Chapman; it is white in color and distinctly segmented, the legs are entirely lacking, and the tracheal system has spiracles on the first and third thoracic and the first six abdominal segments and accessory longitudinal trunks in the thorax.

The mature, and presumably third-instar, larva is known in *Macrosaigon flabellatum*, *Metoecus paradoxus*, *Ripiphorus stylopides*, and *Ripidius pectinicornis*. These present considerable differences, the last-named being markedly different from the others. In *Macrosaigon flabellatum* (Fig. 233*A*), the body is rather elongate and greatly curved, with large fleshy processes on all segments, and the legs are short, fleshy, and nonfunctional. Open spiracles occur on the mesothorax and on the first seven abdominal segments, and atrophied spiracles are found on the metathorax and on the eighth abdominal segment. The larva of *Metoecus paradoxus* is also rather elongate, with the head and thorax sharply bent ventrally and the caudal segments tapering and likewise curved ventrally. A number of fleshy tubercles occur upon the thoracic segments, and the legs are rudimentary, being conical, somewhat pointed, and divided by mere constrictions into three parts. There are eight pairs of spiracles, situated as in the second instar. The mature larva of *Ripiphorus stylopides* is figured by Böving and Craighead (1930) and presents several features that distinguish it from *M. paradoxus*. Two pairs of large fleshy conical processes occur dorsally and dorso-

laterally on each body segment, and the eight pairs of spiracles are situated as in *Macrosaigon flabellatum.*

In contrast to the larvae already described, that of *Ripidius pectinicornis* (Fig. 237) may be considered as intermediate between them and the normal coleopterous larva. The fleshy segmental processes are lacking, and the legs (Fig. 237*c*) are larger and distinctly four-segmented and terminate in a well-sclerotized claw-like tarsus. The head and mouth structures are much reduced (Fig. 237*a*, *b*), the antennae being short and two-jointed, and the most conspicuous feature is the labium, which terminates in three-jointed palpi. No mandibles are discernible. Dorsally on the head there is found a pair of curved, converging, heavily chitinized ridges, which are present also, though widely separated, on the thoracic segments. They are believed to serve in perforating the integument of the host at the time of emergence from the body. Such an adaptation is not required in the species that develop externally upon hymenopterous larvae.

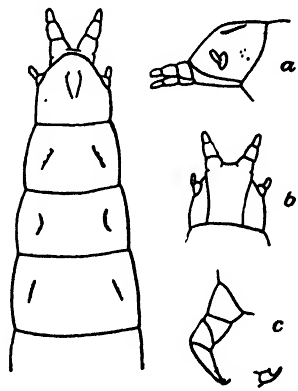


FIG. 237.—The head and thorax, dorsal view, of the mature larva of *Ripidius pectinicornis* Thbg.; *a* and *b*, the head, lateral and ventral views; *c*, a leg, with claw enlarged. (*From Stamm*, 1935, '36.)

MELOIDAE

The oil or blister beetles constitute one of the most common and widely distributed groups of Coleoptera. The adults of many species show a marked reduction in the elytra, and some have lost the hind wings entirely.

HOST PREFERENCES

The food habits of the family are remarkable in several respects. The adults are entirely plant feeders, some species being major pests of cultivated crops, whereas the larvae are parasitic or predaceous and none is known to subsist upon plant food. The greater number of species of which the food preferences are known develop as predators in the egg pods of various Locustidae. These species belong principally to the genera *Zonabris* (called *Mylabris* by many authors) and *Epicauta*, though a few species of *Macrobasis* and *Tetraonyx* have the same habit. A slightly smaller number of species, but representing many more genera, are parasitic in the cells of various bees of the families Megachilidae and Andrenidae. The subfamily Nemognathinae is limited entirely to the latter group of hosts. The more common species occurring upon these hosts are included in the genera *Apalus*, *Meloe*, *Nemognatha*, *Sitaris*, *Zonitis*, *Hornia*, and *Tricrania*. In the majority of cases, the relationship is not true parasitism, in which an individual larva consumes the body contents of the host and completes its development thereon; instead, the egg of the host is consumed, and feeding thereafter is upon the food mass stored in the cell by the parent bee. Balduf (1935)

has given a complete compilation of the host preferences of members of the family, so far as they are known.

It is noteworthy that, in its host preferences, this large family should be limited strictly to the two widely separated groups previously mentioned. The adaptations necessary to gain access to the host stages and to develop successfully upon them are markedly different; and the lack of transitional forms, possibly upon other hosts, is surprising. The two host groups, however, have one thing in common: the stages attacked occur very largely in the soil, though a few species inhabit galleries in wood.

The question of the economic status of the family as a whole is debatable. Unquestionably, the many species that develop in locust egg pods destroy vast numbers of eggs each year, but the actual effect of this upon the host population in its destructive phases is problematical. The numerous species that develop in the cells of bees may markedly reduce the size of the colonies and thus result in less complete pollination of the blossoms of various plants and trees. Though no species is known to attack the immature stages of the honeybee, yet it is recorded in Europe that the triungulinids at times congregate upon the adults in such numbers as to cause marked irritation and death; this occurs so frequently as appreciably to deplete the population of the hives. The most serious injury inflicted by the family is the feeding of the adult beetles upon the foliage and blossoms of cultivated crops, resulting at times in severe injury or necessitating expensive spray applications.

FIG. 238.—An adult of *Zonabris pustulata* Thbg. (*From Verbeek*, 1932.)

Several species of the genus *Horia* are known to develop at the expense of xylocopid bees, and these may be added to the list of beneficial forms. *H. maculata* Swed. was introduced into Hawaii from Guatemala in 1934 for the control of *Xylocopa*, but it is not known to have become established.

BIOLOGY AND HABITS

For a long period of time, the manner of development of the immature stages remained obscure in spite of the abundance of species in all parts of the world. DeGeer first mentioned the parasitic relationship with the Hymenoptera in 1775, and Newport (1845) determined that the triungulinids were carried into the nest by the bees and described the later instars from the cells of *Anthophora*. The latter author's following publications (1846, '53) gave more complete details on the biology and

habits of *Meloe cicatricosus* Leach as a parasite of *Anthophora*. Deposition of the eggs in the soil, carriage of the young larvae to the nest upon the bodies of the adult bees, and development upon the immature stages and upon the food stored in the cell were indicated, though the latter points were not conclusively proved. Fabre (1857) markedly advanced the knowledge of the habits of the group through his study of *Apalus muralis* Foerst., which develops likewise in the cells of *Anthophora*. Carriage of the larvae into the nest was demonstrated, as well as the manner of transfer of the larva to the egg of the bee. Further corroboration regarding the mode of life of the group attacking bees was given by Valery-Mayet (1875) in his account of *Apalus analis* Schaum. (*Sitaris colletis* V.-M.). It was not until the appearance of Riley's (1878*b*, *c*) thorough studies of *Epicauta vittata* F. and other species of the genus that the status of the group as predators upon locust eggs was realized. This author also presented a full account of the striking metamorphosis undergone by the larvae in the course of their development. The more extensive accounts of the biology of representatives of the family that have appeared since Riley's outstanding contribution have been those by Beauregard (1890), Cros (an extended series of papers, 1910 to 1931, only a few of which are discussed), Roepke (1917), Milliken (1921), Parker and Böving (1924), Zackvatkine (1931, '34), Verbeek (1932), and Ingram and Douglas (1932).

Oviposition.—The oviposition period is relatively short in most species and is usually complete in about two to four weeks. The gestation period is short, covering only a few days at most, and in some instances eggs are deposited on the day of adult emergence. The number of eggs that are deposited varies markedly among the different species. The species which develop upon locust eggs usually produce a comparatively small number, ranging from less than one hundred up to several hundred. They are laid in batches in shallow burrows in the hard, dry soil of the breeding grounds of the host, and the burrows are filled and covered when oviposition is complete. The eggs bear an adhesive material which usually causes them to mass together.

In the case of the species that attack bees, the number of eggs produced by each female is considerably larger, presumably owing to the greater hazards encountered by the young larvae before they reach the host cells, resulting in a higher mortality. *Meloe cicatricosus* and *M. autumnalis* var. *cribripennis* Dej. deposit 3,000 or more eggs, and some other species approach this figure. Cros (1931) records that a single batch of eggs of *M. violaceus* Marsh contained 3,000 to 4,000, and several additional batches, containing smaller numbers, were deposited by the same female. One female of *Meloe*, upon dissection, was found to contain a total of 4,218 eggs (Newport, 1851). *Meloe majalis* L. (Cros, 1912, '13)

is said to deposit several thousand in each batch. The first batch usually contains the largest number of eggs, and those following are successively smaller. Each batch represents the entire quantity of mature eggs in the body of the female at the time of deposition, and the abdomen consequently becomes much shrunken. A period of feeding then ensues, and it again becomes gradually distended with eggs.

The place of oviposition of the species attacking bees is not nearly so uniform as that of the species that prey upon locust-egg masses. In *Tricrania sanguinipennis* Say (Parker and Böving, 1924), which develops in the nests of *Colletes*, the batches of eggs are deposited in the soil in the vicinity of the host nests. *Meloe autumnalis cribripennis* (Cros, 1914), *M. majalis*, and *Apalus muralis* (Cros, 1910) have a similar habit. *Hornia nymphoides* Esc. (Cros, 1913), on the other hand, deposits batches of eggs numbering several hundred in the gallery of *Anthophora* or in an old cell, and *Horia debeyi* Fairm. places them in the galleries of xylocopid bees. In the case of *Nemognatha chrysomelina* L. (Cros, 1912), they are found in small batches upon the blossoms of *Echinops spinosus*, and hatching coincides in time with the complete opening of these blossoms. *Apalus rufipes* Gory deposits them upon the blossoms of *Ballota hirsuta* (Cros, 1913). Parker and Böving state that the Nemognathinae, which are restricted in their host preferences to bees, exhibit less care for the safety of their egg masses than do other groups of the family. Some species of *Sitaris*, *Apalus*, and *Stenoria* deposit their eggs in uncovered piles in small grooves in the gallery of the host, whereas others place them on leaves or stems of various herbaceous plants.

The period of incubation ranges from a minimum of four to six days in the case of *Zonitis immaculata* Ol. to about four weeks in other species under normal temperature conditions. Considerably longer periods, up to five months, are recorded for species that oviposit during the cooler seasons or that pass the winter in the egg stage.

Activities of the Larva.—The triungulinids of the majority of species disperse almost immediately after hatching; yet in certain species there is a marked tendency for them to remain en masse for some time about the egg shells. According to Fabre, those of *Apalus muralis* remain thus clustered together throughout the winter. Under normal summer conditions, the young larvae of most species are able to continue their activities without food for a period of three to four weeks. Rau (1930) found several colonies of triungulinids of *Hornia minutipennis* Riley in the vicinity of *Anthophora* nests, and these remained intact for two weeks, even under outdoor conditions during June. When disturbed, however, they attached themselves readily to various objects.

In his early observations upon *H. minutipennis*, Riley (1877) noted that the adult females were found in the immediate vicinity of the host

cells, and it is stated that they probably seldom or never leave the host gallery. Rau has extended our knowledge on this point and records the finding of adult females within host cells; some of them also contained many young larvae. Upon examination, the cells were found to be unbroken except for a minute hole to the outside, which was too small either for emergence or for entry of an adult beetle. Two possible explanations may be given for the occurrence of triungulinids in these cells. Either the female is fertilized through the minute opening mentioned, or reproduction is unisexual.

The means employed by the triungulinids to gain access to the host stages upon which they are to develop are variable. Those which attack locust-egg masses are already in the soil in the breeding grounds of the host upon emerging from the eggs and consequently are dependent only upon their own unaided search to find the egg masses. Likewise, the species that deposit their eggs in the galleries or cells of bees have little difficulty in this respect. In *Tricrania sanguinipennis*, which places its eggs in the immediate vicinity of the *Colletes* nest, Parker and Böving found that the young larvae could not be induced to enter the burrow directly. Instead, entry is accomplished by carriage upon the body of the adult bees. Here the male bees play an important part in the economy of *Tricrania*. They appear in the field about one month earlier than the females, and during this period the parasite larvae are active. Many of them consequently attach themselves to the bodies of these males. The latter are much more active than the females, and for this reason the majority of the parasite larvae are eventually found upon them. It then becomes necessary for the triungulinids to effect transfer to the females in order to reach the brood chamber. It is believed that transfer of the triungulinids from the male to female bees is accomplished at the time of mating; this conclusion is supported by their position upon the bodies of the bees, they being found most abundantly on the venter of the males and on the dorsum of the females.

In the species that oviposit entirely apart from nests of the host bees, the triungulinids often have a strong tendency to climb upward and in consequence may congregate in large numbers upon blossoms. These are frequented by the bees in their search for food, and the larvae attach themselves and are thus carried to the nest. The hatching of the eggs of *Nemognatha chrysomelina* that are deposited upon the blossoms of *Echinops* (Cros, 1912, '19) coincides in time with the complete opening of the blossoms and gives the maximum opportunity for the young larvae to attach themselves to *Anthidium* and other bees that frequent the blossoms of this plant. Usually, they attach themselves to the hairs of the carrier bee, though Cros (1927) states that the larvae of *Meloe cavensis* Pet. cling to the intersegmental folds of the abdomen. Under

the conditions previously mentioned, it is evident that the vast majority of triungulinids will never succeed in reaching host cells; this great loss is accordingly compensated for by the production of a proportionately larger number of eggs among the species subjected to these hazards.

The difficulties encountered by the triungulinids incident to gaining entry into the bee cell in which development is to take place are added to by the necessity for transfer from the body of the female bee to the newly laid egg. This is supposed to take place at the time of oviposition by the bee. In all probability, the triungulinids are largely brushed off against the wall of the cell and then reach the egg by their own efforts. It may be mentioned, however, that the triungulinid of *Tricrania sanguinipennis* is able to let itself down by a silken thread, much after the manner of many lepidopterous larvae, though in this instance the thread originates from the caudal end of the body.

The question arises as to the reason for immunity from parasitization of certain species of bees that are found in the same habitat as others that are heavily attacked. Parker and Böving investigated this point in their studies upon *T. sanguinipennis*, which develops in the cells of *Colletes rufithorax* Swenk but not in those of *Andrena perplexa* Smith, though the nests of the two species were intermingled. This was particularly puzzling because triungulinids were often found upon the bodies of *Andrena* females. The explanation was found to lie in the different oviposition habits of the two species of bees. In *Colletes*, the egg is attached to the side wall of the cell immediately above the food mass, and the parasite larva is consequently able to reach it without coming in contact with the food mass. That of *Andrena*, on the other hand, is placed on end in the center of the food mass, never in contact with the walls of the cell, and is almost completely immersed in thin, watery honey. Any larvae that may gain entry into the cell are effectively prevented from reaching the egg by this liquid barrier.

After gaining access to the cell of the host bee, the first act of the triungulinid is to commence feeding upon the egg. This provides food for the parasite and at the same time eliminates the host, leaving the food supply with which the cell is stocked for the later stages of the parasite. The first molt normally takes place immediately after the host egg has been consumed, and the following instars, being boat-like in form, are able to float freely upon the honey and feed upon it. That the host egg is not essential to the development of the first-instar larva is shown by the fact that one individual of *T. sanguinipennis* was reared to maturity solely upon pollen and honey. Cros found that even the first-instar larvae of a number of species readily accepted honey as well as host eggs and larvae. It often happens that several triungulinids gain access to a single cell, but in no instance does more than one attain

maturity. The youngest individual, being more agile and aggressive, is readily able to overcome those which have molted or which have fed sufficiently to render them sluggish.

In most instances, larval maturity is attained in the cell to which the larva first gained entry. There are certain exceptions to this rule, however; it is recorded by Cros that *Meloe autumnalis cribripennis* may devour the contents of one-half dozen cells during its feeding period and that the fourth-instar larvae of *Nemognatha chrysomelina* and *Zonitis* sp. penetrate into a second cell to complete their feeding. Iwata (1933) mentions that after consuming the food in one cell of *Megachile sculpturalis* Smith the larva of *Z. pallida* F. penetrates the resinous partition of the adjoining one, feeds extensively upon the mature larva contained therein, and finally returns to its original cell, after which it repairs the break in the partition.

The feeding habits of the species that attack locust egg masses are much more simple, inasmuch as the food consists solely of eggs and a sufficient number are present in each mass to provide for the full requirements of the larva. One or two eggs only are eaten prior to the first molt. These larvae are strictly entomophagous during the entire feeding period, in contrast to the habits of the species that develop at the expense of bees.

In practically all species, the first four larval stages represent the feeding period, and the following two are inactive and serve as a resting period or to carry the species through the winter or through periods of adverse temperature and moisture conditions. At the completion of the scarabaeoid stage, the larva may either leave the egg capsule and transform to the following instar in a cell in the soil near by or it may go through its following transformations while still within the capsule. In several species, the coarctate larva is found in a vertical position, with the exuviae forming a pad about the tip of the abdomen. The larva remains in this instar until suitable conditions for further development prevail. Milliken cites the change of *Epicauta sericans* Lec. from the coarctate to the scolytoid stage within a few minutes after the application of water to the body. The scolytoid larva exhibits some degree of activity for several days.

The coarctate larva represents essentially a resting stage in which the species is able to withstand adverse conditions to a remarkable extent. The integument is heavy, thus giving protection from winter conditions in some species and from extremely arid conditions in others. In a number of species, a portion of these larvae consistently persist until the second year, and Zackvatkine states that in *E. erythrocephala* Pall. the diapause may extend over many years. He also mentions that the larvae may, under certain conditions, revert to the coarctate form several

times. This reversion was also noted by Milliken to occur in *E. sericans* Lec., and the occurrence of definite supplementary molts was established by the finding of the exuvia. That portion of the family comprising the predators upon locust eggs thus shows a perfect adaptation, unequaled in any other group of similar food habit, for life under the most adverse conditions.

Among the species that attack bees, the sixth-instar larva is enveloped by the unbroken fourth and fifth exuviae. Because no food is taken after the fourth molt, the body volume decreases somewhat, and the exuviae are consequently not distended. In *Zonitis* and *Nemognatha*, the sixth exuviae are also retained complete, the pupa consequently being enveloped in three larval skins, whereas in other genera of Nemognathinae the last larval skin is found as a pad attached to the tip of the abdomen. The retention of the exuviae in these species may be correlated with the less specialized forms of the last two larval instars, which are much less adapted to adverse conditions than are those of the species subjected to free life in the soil.

Life Cycle.—There is considerable variation in the duration of the life cycle among the various species. The minimum is that for *E. lemniscata* in Louisiana, where development from egg to adult is accomplished in 35 to 50 days and three generations may be produced each year (Ingram and Douglas, 1932). *E. vittata* is said to have two generations annually, as is true also of *Meloe majalis* and *Hornia nymphoides*. *Cerocoma vahli* F. apparently requires about three years for its cycle (Cros, 1919, '24). Perhaps the majority of species have a single generation each year, correlated with the cycle of the host, with the adults appearing during the oviposition period of the latter. *Apalus muralis* is stated to have only one generation in two years, and in a number of species having an annual cycle a considerable portion of the larvae persist until the second year or even longer.

The duration of the various immature stages is correspondingly variable, particularly the nonfeeding periods. The incubation period may range from four or five days to six weeks, and the triungulinid, after a free-living phase that may cover three or four weeks, spends an additional week or more in feeding before the molt takes place. The most uniform figure available is that for the feeding period, comprising a portion of the first larval stage and all of the following three. This covers three to five weeks. The caraboid stage has been determined in several species to require about one week, and the two scarabaeoid stages total approximately the same. The coarctate or pseudopupal stages are those in which hibernation or diapause takes place most frequently; consequently, they vary greatly in length, even within a species. In *H. nymphoides*, it was determined by Cros that a portion of the eggs of the second generation

may carry over until the following spring. Fabre found that the triungulinids of *A. muralis* persist in dense clusters through the winter, whereas a few species hibernate in the adult stage in the cells of the host. The scolytoid stage of *E. vittata* is said to cover only a few days, whereas in *E. lemniscata* it requires 11 to 21 days and is extended in *Zonabris pustulata* Thbg. to 10 to 60 days (Verbeek, 1932). The pupal stage of *Z. zebraea* is two weeks and of *Tricrania sanguinipennis* 24 days.

An unusual variation in habit has been noted in *E. lemniscata*, predaceous upon grasshopper eggs, by Ingram and Douglas. In the summer generation, development through the immature stages is rapid and the scarabaeoid larva changes directly to the pupa, omitting the coarctate and scolytoid stages. In the overwintering generation or under unfavorable conditions, these two stages appear. In *Macrobasis immaculata*, also, these two instars are stated to be lacking.

IMMATURE STAGES

The eggs of the different species of the family are quite consistent in form, being somewhat cylindrical and three or four times longer than wide, and with both ends smoothly rounded. The chorion is delicate and unsculptured, and the color ranges from white to yellow and orange. The size of the egg is governed not only by the size of the beetle itself but by the number produced by the particular species. Thus, in a species that produces 3,000 to 5,000 eggs, they are markedly smaller than in one that deposits only a few hundred.

The larvae of the Meloidae pass through a rather striking metamorphosis in which six instars are usually recognizable. Riley (1883) has proposed that they be designated as follows:

Triungulin—first-instar larva.
Caraboid (Carabidoid)—second-instar larva.
Scarabaeoid—third- and fourth-instar larvae.
Coarctate—fifth-instar larva.
Scolytoid—sixth-instar larva.

These distinctive forms are readily recognizable in all species which develop in locust-egg masses, but the later instars are not so well-differentiated in those which attack bees. Among the latter, the coarctate larva has been variously termed the pseudolarva, pseudonymph, pseudopupa, and pseudochrysalis.

The first-instar larva has attracted the interest of entomologists for a long period of time, and for many years its identity was not established. It was at first considered to be an adult insect, externally parasitic upon bees; it was named *Pediculus apis* by Linnaeus, and later the genus *Triungulinus* was erected for it by Dufour. The term "triungulin," later modified to "triungulinid," has consequently been used to designate the larvae of the family; the reference is to the three claws borne at the end of the tibia in the forms described. This character is not constant throughout the family as pointed out by Cros (1917) and Böving (1924), there being a wide variation among the different species, and the term is not applicable to a considerable portion of the family. Several later authors have used the term "primary larva" instead, but this is likely to lead to confusion, for it generally indicates a host-parasite relationship. In all essential respects, this larva is of the true planidium type, having the distinctive features and habits of larvae of the Perilampidae, Eucharidae, Cyrtidae, Ripiphoridae, and Strepsiptera.

The body of the first-instar larva (Figs. 239*A*, 240*A*) is fusiform, is broadest in the thoracic region, and has the nine abdominal segments successively narrower. It is white, yellow, or orange at the time of hatching; but the integument quickly darkens, often becoming almost black. The head and thorax combined are approximately equal to the abdomen in length. In outline, the head varies from triangular to quadrangular. The black ocelli, either simple or double, are situated near the lateral margins. The mandibles range from the simple falcate form to those having up to 12 teeth, the more strongly dentate forms being of species that attack locust-egg masses. The antennae are large, cylindrical, and three-jointed; the second joint is longest and bears a sensory organ, and the third terminates in a spine that may vary in length from half to six times that of the entire antenna. The thoracic segments are long and heavily sclerotized, and the legs comprise four principal joints, with the tibia terminating in a simple claw-like tarsus, with a pair of setae of varying size at the base,

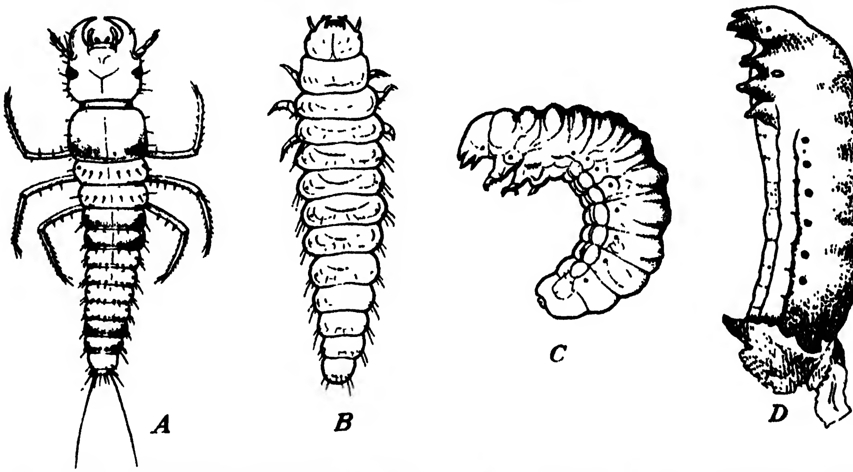


FIG. 239.—The larvae of *Epicauta vittata* F. *A–D*, the first, second, fourth, and fifth instars. (*From Riley*, 1877.)

or in a "trident of Neptune" structure, to which the term "triungulin" refers. The lateral processes, however, have no muscle attachments.

The abdominal segments in many species have the tergal and pleural plates heavily sclerotized and indurated, whereas the skin of the intersegmental areas is delicate and white in color. The body consequently has a distinctly banded appearance after becoming distended with food. In many of the species that attack locust-egg masses, this coloration of the segments is not nearly so distinct. One pair of caudal cerci is found usually, though not always, on the ninth abdominal segment, these being very short in some species whereas in others their length may exceed half that of the abdomen. In a few species, a supplementary pair is found on the eighth segment. The various body segments may bear a number of short setae, usually arranged in transverse rows. The abdomen terminates in a somewhat bulbous adhesive disk which is utilized in clinging to the substratum. By means of the erectile caudal cerci, aided by the adhesive disk, the triungulinid is able to assume an upright position when stimulated by the approach of a carrier, a habit that is general among larvae of this type in several orders.

The data available indicate that the number of pairs of spiracles may be seven or eight, with the first pair occurring on the mesothorax and the remainder on the succes-

sive abdominal segments. In a number of species, those of the mesothorax and the first abdominal segment are very large, and the remainder minute. Several species are known to have the spiracles of the eighth abdominal segment borne at the tips of a pair of falciform processes, which are considered to provide against the entry of fluids into the tracheal system.

The second-instar (caraboid) larva (Fig. 239*B*) differs from the preceding instar principally in its more robust body and reduced head and legs. The heavily sclerotized and indurated integument is replaced by a rather delicate, white skin. In *Tricrania* (Fig. 240*B*) and others that attack bees, the body assumes a distinctive boat-like form

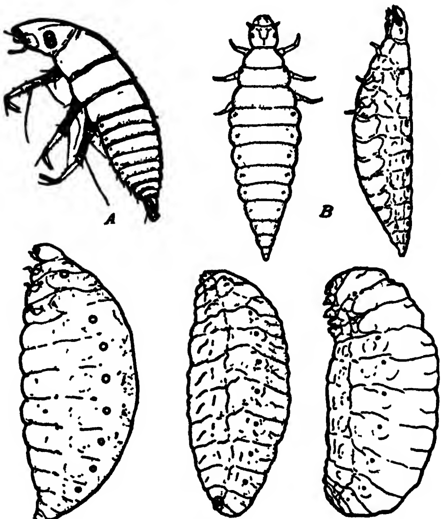


FIG. 240.—The larvae of *Tricrania sanguinipennis* Say. *A*, the first instar; *B*, the second instar, dorsal and lateral views; *C–E*, fourth, fifth and sixth instars. (*From Parker and Böving*, 1927.)

in which the dorsum is nearly flat and the venter markedly convex, enabling it to float readily upon the surface of the food material in the cell. This modification in form is accompanied by a shift in the position of the spiracles, which become markedly dorsal. The antennae are now somewhat conical in form and lack the long terminal setae. The integumentary setae may persist, particularly in the species attacking locust-egg masses, but they are reduced in size.

The third- and fourth-instar (scarabaeoid) larvae (Fig. 239*C*) of the species attacking locust eggs are quite similar in all respects and have a striking resemblance to the grubs of Scarabaeidae. The abdomen is much increased in size, and the legs are further reduced. In *Tricrania* (Fig. 240*C*), *Apalus*, and others of the Nemognathinae, the third instar is quite similar to the second, retaining its boat-like form, but in the fourth instar the abdomen is greatly distended and markedly convex dorsally as well as ventrally.

The fifth-instar (coarctate) larvae of *Epicauta* (Fig. 239*D*) and others of similar host preferences are markedly different from the preceding instars in having the legs rudimentary, represented by conical protuberances only, the mouth parts likewise rudimentary and not serving for feeding purposes, and the body segmentation often indistinct. A pronounced longitudinal ridge extends along the lateral margins of the first seven abdominal segments. The integument is much heavier than in the preced-

ing instars and bears transverse corrugations. Among the species of Nemognathinae and other groups attacking bees, this instar (Fig. 240*D*) is not nearly so distinctly differentiated, though the mouth parts and legs are greatly reduced and functionless. The term "coarctate" is not properly applicable to all larvae of the family of this instar, inasmuch as many are not enveloped by the exuviae.

The sixth-instar (scolytoid) larva is so named because of its resemblance to the larvae of the Scolytidae, and it consequently represents a reversion to a form somewhat similar to the scarabaeoid. It is of reduced size as compared with the two preceding instars, owing to the last two transformations having been accomplished without feeding. The legs, though still largely functionless, are relatively larger than before.

PYTHIDAE

Several species of this small family are recorded as being predaceous upon bark-beetle stages in Europe. Some have very active larvae which are similar in general form to those of the Carabidae.

ANTHICIDAE

The larvae of several species have been noted to develop as predators upon the immature stages of other insects, some apparently being strictly predaceous in habit, whereas others are scavengers or plant feeders. Howard (1896) gives an account of *Anthicus heroicus* Casey as an enemy of the sialid, *Corydalis cornuta* L. This neuropteron deposits its eggs during midsummer, in large masses numbering several thousand and covered with a tough, calcareous substance, upon leaves or other objects overhanging or near water. Both the larvae and adults of *Anthicus* feed extensively upon these eggs, and a dozen or more may be found in a single egg mass. The female beetle presumably gnaws a hole in the egg mass, in which she places her own eggs. Upon completion of feeding, the larvae enter the soil or rubbish for pupation. There are evidently several generations each year, and hibernation is in the adult stage. Gill records *Notoxus monodon* F. as feeding upon the pupae of *Archips* in rolled leaves.

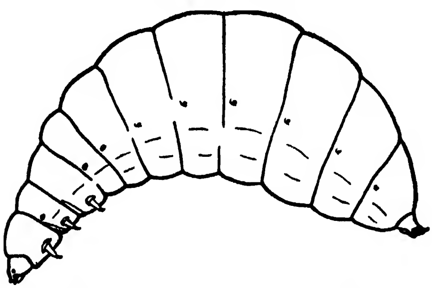


FIG. 241.—The mature larva of *Sandalus niger* Knoch. (*From Craighead*, 1921.)

RHIPICERIDAE

The information available regarding the habits of this small family is very limited. Craighead (1921) reports taking a mature larva of *Sandalus niger* Knoch. (Fig. 241) from a pupa of *Cicada* that had made its emergence burrow and reached the surface of the soil. It evidently had developed as a parasite, and its body showed modifications, such as a

reduction in the legs, consequent upon this mode of life. It is quite robust in form, and the ninth tergum has a sclerotized tip and bears a pair of broadly conical cerci.

ELATERIDAE

This family is well-known because of the plant-feeding habits of the larvae of a great majority of species, a number of which are major crop pests. A considerable number of genera, however, contain species that are predaceous upon insects rather than being of phytophagous habit. As the larvae are largely soil inhabitants, they feed upon such other soft-bodied insects as they may encounter. Thus scarabaeid grubs are among the most frequent victims of these species. *Monocrepidius pallipes* Esch. is said to be one of the most important of the natural enemies of white grubs in Fiji and has not been observed to attack cane, whereas *M. exsul* Sharp, though known to prey upon grubs, is destructive to young sugar-cane plantings in various Pacific islands (Williams, 1931). The conspicuous "cucubano" of the West Indies, *Pyrophorus luminosus* Ill., serves as a check upon various cane grubs of the family Scarabaeidae and has been imported into several tropical countries in the attempt to control various pests belonging to this group. A number of species inhabit decaying wood and prey upon the larvae of various xylophagous insects.

HELODIDAE

Little is known about the food habits of this family, the better known species of which are aquatic in the larval stage. The larvae of occasional species are said to feed, in part at least, upon other insects that they encounter.

DERMESTIDAE

The members of the family are known to feed upon dead animal and plant materials, more particularly the former. A number of species, however, are known to feed upon the eggs of other insects, especially where they are enclosed within a distinct case or in a compact mass with a felted covering. The larvae of several species of *Thaumaglossa* have been observed feeding in mantid-egg cases in Texas and South Africa, and in Japan a high percentage of those of *Tenodera sinensis* Sauss. were found infested with an undetermined species. A considerable number of larvae may be found in each case, and the entire contents are usually eaten out before the end of the incubation period, which covers at least six months. In certain parts of Europe and North Africa, *Dermestes*, *Trogoderma*, and *Attagenus* are reported to be important predators upon the eggs of the gypsy moth and other Lepidoptera having similar egg masses, and several species of *Dermestes* seriously infest the cocoons of silkworms in

Europe and Asia, though presumably they do not attack the living larvae or pupae contained in them.

OSTOMIDAE

Relatively little is known regarding the entomophagous habits of the members of this family. A number of species of several genera have been noted to prey upon the larvae and pupae of bark- and wood-inhabiting beetles, some being reported to be of considerable importance because of this habit. The well-known cadelle, *Tenebroides mauritanicus* L., which is primarily a feeder upon grains and grain products, is also a general predator upon other insects that inhabit the same medium.

NITIDULIDAE

The predaceous habit is known to occur in several genera of the family. *Carpophilus mutilatus* Erich. is mentioned as an extensive feeder upon aphids on corn in Barbados. Apparently, all species of the genus *Cybocephalus* are predaceous, in both the adult and larval stages, upon Coccidae, most frequently of the Diaspinae. In 1882, C. V. Riley reported two species as predaceous upon *Chionaspis* in western North America. *C. flavipes* Reit. and *C. seminulum* Baudi are credited with effectively controlling *Parlatoria blanchardi* Targ., in North Africa (Balachowsky, 1928). The first-named is strictly a desert-inhabiting species and consequently is well-adapted for life in the date-growing countries of North Africa and the Near East. Several generations are produced each season, and the adults are present throughout the year. *C. californicus* Horn is recorded as an aggressive predator of the cypress bark scale, *Ehrhornia cupressi* Ehr., in California.

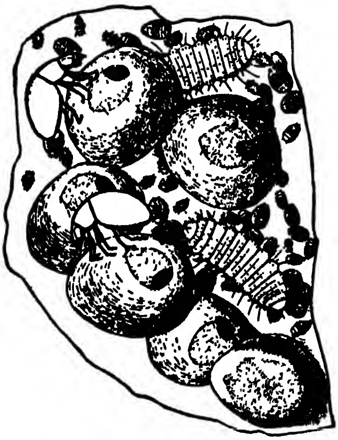


FIG. 242.—Adults and larvae of *Cybocephalus rufifrons* Reit. feeding upon *Aulacaspis pentagona* Targ. (*From Silvestri*, 1910.)

According to Silvestri (1910*a*), the females of *C. rufifrons* Reit. deposit their eggs beneath the female scales of *Aulacaspis pentagona* Targ. and at times among the newly hatched larvae that have not yet left the protection of the scale covering. A thin-walled cocoon is spun upon the foliage by the mature larva, and this is covered with the remains of host insects and other extraneous material.

Cybocephalus sp. is a predator upon the larger larvae and pupae of several species of *Aleurocanthus* in Java (Clausen and Berry, 1932). The

larvae, which are white in color, are sluggish in habit and remain upon the same leaf during the entire feeding period, provided that sufficient food is available. They have a marked resemblance to larvae of several species of the coccinellid genus *Scymnus* which attack the same host. Pupation takes place in a cell in the soil rather than upon the foliage, and no cocoon is formed.

RHIZOPHAGIDAE

Very little is known regarding the insect-feeding habits of this family beyond the genus *Rhizophagus*, the species of which are predaceous upon bark beetles. Several species have been imported into Canada and New Zealand from Europe in the attempt to control various Scolytidae. *R. parallelicollis* Gyll. has been recorded in several instances as a carrion feeder and has been termed the "graveyard beetle" because of its supposed feeding upon human corpses. More recent studies by Blair (1922) indicate that it is more probably predaceous upon the larvae of Phoridae occurring in the same habitat.

CUCUJIDAE

A wide range in food habits is revealed among the members of the family. As in a number of related families, development of many species takes place in grain and grain products. Sheppard (1936) found that the cosmopolitan *Cryptolestes ferrugineus* Steph., which feeds upon whole or milled grain, is at times predaceous upon other insects or scavengerous upon their dead bodies. The highest oviposition rate was secured from females fed only upon angoumois grain moth eggs, and larval development was most rapid when insect food was provided. A considerable number of species, however, are strictly predaceous and attack the wood-inhabiting Coleoptera, principally the Scolytoidea, whereas others that attack the same host group are in part phytophagous. Several species have been noted to feed upon termites.

COLYDIIDAE

The available information regarding the feeding habits of this rather uncommon family is limited. Some species are known to feed solely upon decaying vegetable matter, a number of species are predaceous upon wood-inhabiting beetles, and a few are definitely parasitic. Craighead (1920) mentions that *Bothrideres geminatus* Say is predaceous upon mature larvae or pupae of several Cerambycidae and that in one instance several larvae were found within a pupa of *Chrysobothris*. In the latter case, development was believed to have taken place internally. Hopkins had previously recorded *B. contractus* as an external parasite of cerambycid

larvae. *B. cactophagi* Sc. has been recorded as parasitic upon the prepupae of the large cactus weevil, *Cactophagus validus.*

Deretaphrus oregonensis Horn was taken by Craighead from the pupal cells of *Asemum atrum* Esch. in pine, the host larvae being full-grown before death. The mature larva of this parasite (Fig. 243) is very appreciably modified because of its host relationships. The body is fleshy, fusiform, and much the widest in the mid-abdominal region and has the integument thin and practically glabrous. The mandibles are triangular and bifid at the apex, and the ventral mouth parts are fleshy and weak. The legs are short, weak, and widely separated. Spiracles occur on the second thoracic and the first eight abdominal segments. The ninth segment bears a pair of chitinous recurved hooks dorsally.

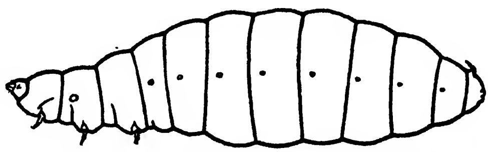


FIG. 243.—A mature larva of *Deretaphrus oregonensis* Horn. (*From Böving and Craighead,* 1930.)

Piel (1938) records *Dastarcus helophoroides* Fairm. as an external parasite of the mature larvae of *Xylocopa appendiculata* Smith in China. The first-instar larva is elongate, indistinctly segmented, and without spines or setae and bears minute rudimentary legs. Development is complete in a minimum of four days. These larvae were found upon hosts that had been killed by mites and were already undergoing decomposition, so that it is uncertain whether they are parasitic or scavengerous. The degenerate form of the larva would indicate that they are of parasitic habit.

MYCETOPHAGIDAE

The larvae of *Berginus maindroni* Grouv. are reported to feed extensively upon the lac insect, *Laccifer lacca* Kerr., and upon the lac itself, in India. Pupation takes place within the egg chamber of the female coccid.

PASSANDRIDAE

The entomophagous habit of feeding is known in several species of this small family and has developed in some into obligate parasitism. Fiske (1905) records observations on *Catogenus rufus* F. which indicate that the larvae are true external parasites of the pupae of certain cerambycid borers and of those of the braconid parasites which attack the same hosts. *Scalidia* is also reported to develop parasitically.

LATHRIDIIDAE

Very little is known regarding the entomophagous feeding habits of members of this family. The adults of *Enicmus minutus* L. are said to feed rather extensively upon the beech scale, *Cryptococcus fagi* Baer., in England.

Extended observations have been made upon the host preferences and habits of the South American *Coccidophilus citricola* Brethes, which is predaceous in its active stages upon diaspine Coccidae (Flanders, 1936*b*). The female places her eggs beneath the host scale covering, and hatching occurs in 8 to 9 days. The larval feeding period covers 10 days, though the stage persists for 13 to 20 days. Pupation takes place in crevices, and the adult beetle emerges 5 days later. At temperatures of 24 to 27°C. the cycle from egg to adult is complete in 27 to 35 days.

PHALACRIDAE

Very little is known regarding the entomophagous habits of members of this family. Fluke (1929) records *Eustilbus apicalis* Melsh. as a very common predator upon the pea aphid, *Illinoia pisi* Kalt., in Wisconsin. The beetles were particularly abundant in alfalfa fields, and the younger aphids were most frequently attacked.

COCCINELLIDAE

The family is world-wide in distribution. In practically every region, various species occur in large numbers, and these, because of their habits, are the most frequently encountered of all the predaceous Coleoptera. The great majority of species are insect feeders, and, as a result of their attack, many plant pests are kept partly or completely under control. A conspicuous exception to this feeding habit is found in the subfamily Epilachninae, which contains a number of species, mostly of the genus *Epilachna*, that are foliage feeders and often cause serious damage to crops, particularly legumes and potato. Species of the tribe Psylloborini feed exclusively upon fungi. The entomophagous forms in the Coccinellinae are predominantly predaceous upon Aphididae, Coccidae, and Aleyrodidae, and the great majority of these pests have one or more species that feed upon them. A small number of species are apparently limited in their host preferences to other groups. Thus, several species of *Aiolocaria* and *Neoharmonia* are effective predators upon all immature stages of certain chrysomelid beetles, whereas other genera and species favor Chermidae and mites.

In the aphid- and scale-feeding species particularly, there is often a pronounced tendency to vary the diet, and many species will be found to feed at times upon immature stages of Lepidoptera, Hemiptera, etc.

Some have been shown to feed extensively at nectar glands of plants and on sap, pollen, fungi, honeydew, etc. (Watson and Thompson, 1933). This is particularly noticeable during times of scarcity of the normal food and may prove to be a more general habit than is now recognized. *Chilomenes vicina* Muls. feeds very extensively upon the eggs and young larvae of the cotton worm, *Prodenia litura* F., in Egypt during periods of aphid scarcity (Bishara, 1934). *Neocalvia anastomozans* Crotch preys consistently upon the larvae of the fungus-feeding *Psyllobora* of the same family, and the opinion is expressed by Camargo (1937) that this unusual habit is general among species of that genus. In Japan, both larvae and adults of *Hippodamia tridecimpunctata* L. are reported by Kuwayama to feed upon the eggs and young larvae of the rice beetle, *Lema oryzae* Kuway., during June and July, at which time the preferred aphid hosts are at a low population level. It is rated as one of the most important of the natural enemies of that beetle. These various changes in food source are very evidently advantageous from the point of view of maintaining the species during times of scarcity of the host insects. A distinct tendency toward cannibalism in both the larval and the adult stages serves the same purpose. For a more complete summary of the food habits of the family, the reader is referred to Schilder and Schilder (1928) and Balduf (1935).

A number of species of the family have been utilized effectively in the biological control of crop pests. The outstanding example is, of course, the Australian vedalia beetle, *Rodolia cardinalis* Muls., which has effectively controlled the cottony-cushion scale, *Icerya purchasi* Mask., and other related species, in many countries. *Cryptolaemus montrouzieri* Muls., a predator upon mealybugs and also of Australian origin, has proved effective in reducing heavy infestations in a number of countries but, probably because of its size, it is not adapted to prey upon sugar-cane mealybugs or others of similar habit, which are protected by leaf sheaths. *Cryptognatha nodiceps* Mshll., native to Trinidad and other tropical American sections, was largely responsible for the complete control of the coconut scale, *Aspidiotus destructor* Sign., in Fiji. An undetermined species, closely related to *Cryptognatha*, was imported into Cuba from Malaya in 1930 and demonstrated its ability to control heavy infestations of the citrus blackfly, *Aleurocanthus woglumi* Ashby, in a very few months. *Azya trinitatis* Mshll. was the most effective of a series of species introduced for the control of *Aspidiotus destructor* in Puerto Rico. It is noteworthy that very little success has been attained in any region through the introduction of aphid-feeding species.

The successful utilization of Coccinellidae against diaspine Coccidae appears to be limited by certain physical characters of the scale covering. Those species of which complete or partial control has been secured are

distinguished by the possession of a relatively thin and readily penetrated covering. Species with an exceptionally thick and tough covering, such as *Lepidosaphes*, *Chionaspis*, and *Prontaspis*, are relatively free from attack by members of this family. Some that are quite polyphagous in habit, in so far as Coccidae with light scale coverings are concerned, have been found unable even to complete development when limited to hosts having a heavy covering.

Although the entomophagous Coccinellidae are generally considered to be strictly predaceous in habit, yet certain species have become quite specialized and may develop as solitary external parasites. This occurs in some species that attack hosts much larger than themselves. Thus, *Novius limbatus* Mats., which attacks all stages of the enormous *Drosicha corpulenta* Kuw. in Japan, is only a fraction of the size of the adult coccid female, and instances have been noted where the egg was deposited beneath the scale and the resulting larva retained its feeding position on the ventral side of the body of the single host until mature and ready for pupation.

The relationship of the coccinellid larva to its host appears to be the factor that determines its effectiveness in reducing the population, and the nearer it approaches the habits of a parasite the more effective it is in controlling the host before it reaches destructive numbers. By virtue of this quality, *R. cardinalis* is able to bring its host to a low numerical level and to hold it at that point. The egg is laid upon the adult *Icerya* female or upon the egg mass, and there is sufficient food material in the egg output of the one female to bring the larva to maturity. Thus the larva is spared the necessity of searching for food, and the species is able to maintain itself in an exceedingly low host population.

The same factor operates in the case of species effective against diaspine Coccidae and Aleyrodidae, though in modified form. These hosts, even when relatively scarce, are gregarious in habit and thus reduce appreciably the need of search for food on the part of the predator larvae. The adult beetle, being an active flier, finds the food on which its progeny are to develop prior to oviposition.

The aphid-feeding species particularly, such as the well-known *Hippodamia convergens* Guer., and also those which attack solitary Coccidae, suffer a great loss through their inability to find a sufficient number of hosts in a low population to bring them to maturity. They are often very effective in reducing heavy infestations; but unfortunately this comes after serious crop injury has occurred, and their value is consequently greatly reduced.

The general host preferences of the family have already been briefly summarized, but certain specific adaptations in host relationships may be cited. The newly hatched larva of *Cryptognatha nodiceps* beneath the

covering of the mature *Aspidiotus* scale usually finds a number of eggs thereunder which have not been devoured by the parent beetle, and these provide its first food. After emergence from beneath the scale covering, it feeds preferably upon second-instar larvae, whereas, following the first molt, attack is upon any stage of either sex of the host (Taylor, 1935). In *Scymnus sieverini* Weise, the young larvae feed mainly upon the young scales of diaspine Coccidae, whereas the nearly full-grown larvae prefer the eggs. The larvae of *Rhizobius ventralis* Er. which hatch from eggs deposited beneath ovipositing *Saissetia* females may feed either upon the eggs or upon the female scale, whereas those which are free upon the foliage attack only the young scales.

The adult beetles invariably attack the same host species that serve as food for the larvae, though a different stage may be favored. They chew their victims vigorously and consume all but the harder portions of the body, whereas the larvae usually bite out a hole in the body wall and suck out the fluid contents. In a number of instances, a marked degree of pre-oral digestion has been found to occur, in which the fluid contents are sucked out and repeatedly pumped back into the body of the victim, thus effecting a rapid and thorough mixing with the digestive juices.

The daily consumption of food by the larvae is roughly proportionate to their size. Feeding records of a series of California Coccinellidae (Clausen, 1916) indicate that the fourth-instar larvae of species of average size, such as *H. convergens*, consume approximately 50 aphids per day and that the adult females, if ovipositing regularly, have very nearly the same capacity. The larva of the giant *Caria dilatata* F. of China is reported to consume 400 to 500 bamboo aphids each day. According to Bishara (1934), *Chilomenes vicina* Muls., which is normally an aphid feeder, destroys up to 22 eggs or 12 to 15 young larvae of *Prodenia litura* F. daily during periods of aphid scarcity. The same habit is recorded for *Coccinella undecimpunctata* L.

The manner and place of oviposition are quite largely dependent upon the type of host insect that is attacked. The majority of species that feed upon aphids, such as *H. convergens*, deposit their eggs in compact clusters of 10 to 50 (Fig. 244), the spindle-shaped eggs standing vertically on the leaf or bark surface. In *Synoncha grandis* Thbg., however, they are spaced at intervals of several millimeters. *Caria dilatata* F., when attacking aphids on bamboo and pine, places the eggs in 2 rows, averaging a total of 28 in each group. When these are placed on the needles of pine, a mucilaginous ring is formed about the needle a few millimeters below the egg mass (Liu, 1933); this is said to provide a degree of protection from predaceous enemies. The red-mite feeders and some of the species attacking diaspine scales deposit the eggs singly or in small clusters, and horizontally, in the immediate vicinity of the hosts. The latter group,

however, more generally places them singly beneath empty scale coverings, the ovipositor being inserted beneath the margin, through a feeding hole previously made by the female, or occasionally through a parasite emergence hole. This habit is especially frequent among those species which attack scales having a soft covering such as is found on *Aspidiotus destructor* and related forms. Species of the genera *Scymnus, Chilocorus, Pentilia, Cryptognatha,* and *Rhizobius* often oviposit in this way. A number of species that attack Aleyrodidae consistently place the eggs singly or in pairs within the pupal cases from which the white flies have emerged. In attacking lecaniine Coccidae such as *Saissetia oleae* Bern., which have a large egg chamber beneath the body of the female, *Rhizobius ventralis* and others insert the eggs beneath the living host adult. The

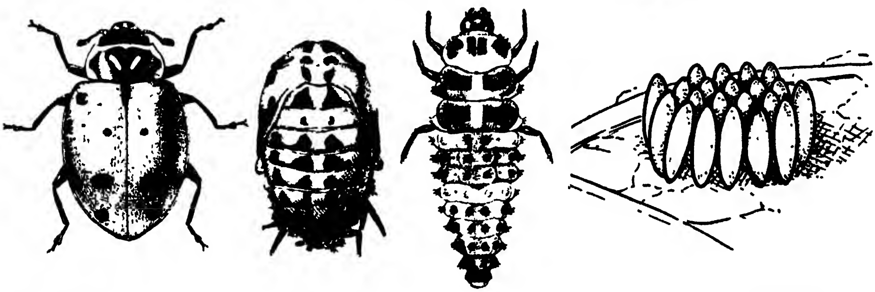


FIG. 244.—A cluster of eggs, and the mature larva, pupa, and adult female of *Hippodamia convergens* Guer. (*All figures except eggs from Chittenden,* 1918.)

mealybug predators normally place their eggs promiscuously among the hosts, directly upon the dorsum of the female scale, or in one of the surface grooves of the egg sac.

The reproductive capacity is often relatively high, the maximum egg deposition recorded being 1,550; this was secured by E. K. Carnes from a female of *H. convergens* during a period of slightly more than two months, and Swezey (1905) secured a maximum of 944 from *Callineda testudinaria* Muls. In general, it may be said that the aphid-feeding species of the genera *Hippodamia, Coccinella, Leis, Callineda,* etc., deposit the greatest number of eggs, ranging from 500 to 1,000 in a number of instances, whereas those which attack Aleyrodidae, diaspine Coccidae, and red mites produce a much smaller number. The duration of the oviposition period is quite long, usually exceeding one month, and instances are known in which it has extended over three or four months. The great extension of this period is quite closely correlated with reduced temperatures and a scarcity of food material. The rate of oviposition is governed by the same factors; it seldom exceeds 10 to 12 per day over an extended period, even in the most prolific species.

Mating usually takes place within 1 or 2 days after emergence, and deposition of fertile eggs begins 7 to 10 days later. Older females that

have had sufficient time for egg formation before mating will, of course, produce fertile eggs in a much shorter period of time. The virgin females of several species have been noted to deposit a much smaller total of eggs than those which have mated. These unfertilized eggs, however, do not hatch. In many instances, only a single mating has been found necessary to ensure fertilization of the eggs deposited during the entire lifetime of the female.

The eggs of the larger aphid-feeding species are quite uniformly spindle-shaped and yellow or orange-yellow in color. Those species which attack diaspine Coccidae, Aleyrodidae, and red mites have eggs with the poles much more broadly rounded; they may be white, yellow,

FIG. 245.—Mature larva, pupa, and adult of *Hyperaspis binotata* Say. (*From Simanton, 1916b.*)

or greenish-yellow in color, with the chorion often bearing minute reticulate markings. The egg of *Cryptolaemus montrouzieri* is somewhat amber in color; that of *Rodolia cardinalis* is distinctly orange-colored. As incubation progresses, there is a noticeable darkening; just prior to hatching, the egg becomes almost black in the species that have dark-colored larvae, whereas in others it becomes grayish. Observations on a number of species indicate that egg color is influenced to a considerable extent by the color of the host insects upon which the female beetles feed.

The appearance and characters of the larvae of the Coccinellidae are so well-known that it is unnecessary to give a detailed description. The larger aphid-feeding species such as *Hippodamia* and *Coccinella* have variable color markings and bear a number of relatively short setae upon the segments, and this is true, also, of many species attacking Coccidae. In *Chilocorus* and related forms, the larvae may bear large, branched fleshy processes on each segment. Others are white in color, with delicate setae. Many species of *Scymnus*, *Hyperaspis* (Fig. 245), *Cryptolaemus*, etc., bear a heavy covering of white waxy material, which may be in the

form of granules, slender threads, tufts, or plates, depending upon the species, produced as a glandular secretion. There appears to be a tendency among the species attacking mealybugs and other hosts having a waxy covering to bear a similar covering themselves. This is stated to be the result of feeding upon hosts having a high wax content rather than being an adaptation for protective purposes. However, some species developing upon diaspine Coccidae have this heavy waxy covering whereas others on the same host do not.

For detailed information on the morphology and classification of the larvae of the family, the reader is referred to the publications by Böving (1917) and Gage (1920).

With very few exceptions, the members of the family have four larval instars, the exceptions being *Pseudonycha japonica* Kuris., which is said by Iwata (1932) to have five instars, and *Hyperaspis lateralis* Muls., in which the autumn generation has only three larval instars in contrast to the normal four of the spring generation (McKenzie, 1932).

Pupation usually takes place *in situ* on the foliage or bark at the point where feeding was completed. *Cryptolaemus montrouzieri*, however, very frequently descends the trunk of the tree and pupates in masses in sheltered places thereon or in trash on the surface of the ground, whereas *Chilocorus similis* (Fig. 246) and others of that genus and of *Cryptognatha* assemble for pupation in large aggregations on the twigs, the lower sides of the main branches, and the trunk.

When the mature larva is ready to pupate, it fastens the caudal tip of the body securely to the substratum by means of a mucilaginous secretion. The aphid-feeding species quite generally cast the final larval exuviae almost completely, and it remains only as a collar or ring about the base of the abdomen. *Cryptolaemus*, *Rodolia*, and some species of *Scymnus* and *Curinus* merely effect a median split of the exuviae over the anterior portion of the body.

The life cycles of the Coccinellidae are relatively short in all cases, though they are considerably lengthened under adverse temperature and food conditions. For this reason, only records secured under optimum summer conditions are comparable. The minimum recorded time from deposition of the egg to emergence of the adult beetle is 12 days in the case of *Propylaea quatuordecimpunctata* L. (Strouhal, 1926), and the great majority of species require 20 to 35 days. The period of incubation covers 2 to 6 days. The first and fourth larval stages are usually slightly longer than the intervening two, and the four total 7 to 30 days, with a general average of about 20 days. The pupal stage is of 3 to 10 days duration, averaging in the neighborhood of 6 days. In the tropics, the generations often succeed each other with little delay, and a new brood may be produced each month, whereas under temperate conditions only

one or two may be produced each season, owing to the short period in which adequate food is available, even though temperature conditions would permit of a larger number. Thus, a species that is limited to a host having an annual cycle and suitable for feeding for only a short period would itself have a minimum number of generations during that period.

The winter is uniformly passed in the adult stage in sheltered places, in large masses in mountain valleys, in smaller aggregations under the bark of trees, in piles of rubbish, beneath stones, etc., or singly in the

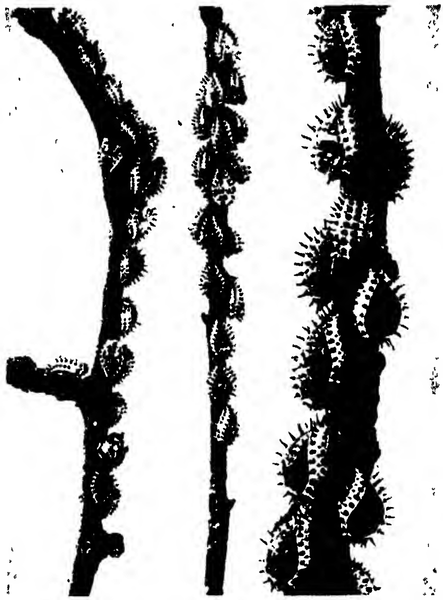


FIG. 246.—Pupae of *Chilocorus similis* Rossi in characteristic colonies on twigs of trees infested with diaspine Coccidae. Those at left and center approximately natural size. (*From Marlatt*, 1906.)

latter locations. The one exception to this habit is *C. montrouzieri*, which passes the winter largely in the pupal stage in dried leaves or beneath the bark of the trees upon which it develops. It is able to persist only in subtropical regions, however, where development during the winter is not entirely inhibited, and some adult beetles may also be found at this time.

The assembling of vast numbers of coccinellid beetles in mountainous regions far removed from the areas in which feeding and reproduction take place is the result of a pronounced tendency toward migration, but the factors responsible for this movement are not well-understood. In the case of *Hippodamia convergens* in western North America, these huge colonies are present at certain points year after year, deeply buried in snow (Carnes, 1912). Frequently, however, they may be found in mountain

valleys during midsummer, massed upon stones and usually near water, under high temperature conditions. This migration and assemblage in large masses have been attributed to several influences, among which are food scarcity, temperature, and air currents. The choice of identical sites year after year may be explained by the presence of large numbers of dead bodies which are left in the spring after the colony has departed and which provide a persistent odor that attracts the beetles in the following autumn. The occurrence of large aggregations of beetles in hibernating quarters in mountainous regions has been recorded in several parts of the world and is the normal habit of a number of species of several genera. Dobrzhanski (1922) discusses the phenomena of gregariousness and migration in the family and concludes that they have a physiological basis and have no relation to shortage of food.

TENEBRIONIDAE

The majority of the species of the family are scavengers, though some feed upon grain or grain products and a few are questionably predaceous. Those which are reported to have the latter habit are found in association with bark and wood borers, but in no instance can the evidence as to food source be considered conclusive.

SCARABAEIDAE

This large family is, as is well-known, almost entirely phytophagous in habit, the larvae living in the soil and feeding extensively upon roots and decaying vegetable matter and the adults attacking the foliage, blossoms, and fruit of many plants. In the genus *Trox*, however, there are a number of species that have developed the carnivorous habit to a greater or less extent. Hayward (1936) gives a short account of *T. suberosus* F. as a predator on the eggs of the locust, *Schistocerca paranensis* Burm., in Argentina. Under favorable conditions, the grubs are stated to destroy nearly 100 per cent of the eggs, and he advocates the use of this predator in the biological control of the pest. Denier (1936) questions the current evaluation of the species and states that caged individuals would not feed upon any living stage of the locust but only upon those which were dead and partly decomposed. The presence of large numbers of beetles at the egg beds is attributed to the presence there of the dead bodies of many locusts.

The dung beetles belonging to this family are of considerable aid in the control of certain pests, such as the Diptera that breed in this medium, through the elimination of the dung before the maggots are able to reach maturity. A number of species, mainly of *Aphodius*, *Canthon*, *Copris*, *Onthophagus*, and *Phanaeus*, have been imported into Hawaii and Puerto

Rico to aid in the control of the horn fly. *Onthophagus incensus* Say has become established in Hawaii.

ANTHRIBIDAE

Information relative to the insect-feeding habits of the family are limited to certain species of *Brachytarsus*,[1] which have been recorded as reared from lecaniine Coccidae.

Yano (1915) was the first to give an account of the predaceous habits and life history of a representative of the genus. His studies dealt with *B. niveovariegatus* Roel. which attacks the Chinese wax scale, *Ericerus pela* Chev., in Japan. Observations during May and June showed that approximately 50 per cent of the female scales contained mature larvae,

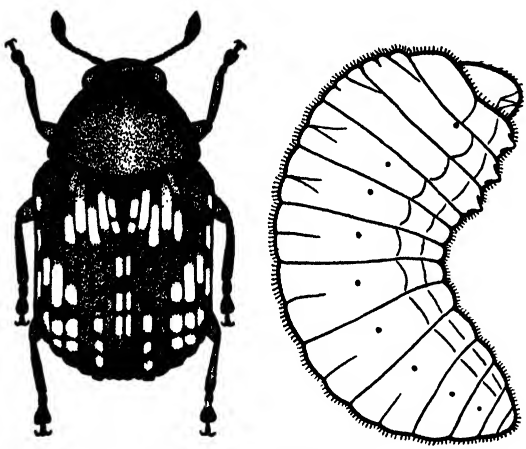


FIG. 247.—The adult female and a mature larva of *Brachytarsus niveovariegatus* Roel. (Original.)

pupae, or adults of the beetle in the egg chamber. The adults emerge during the latter part of June, and the remains of the host scales are then conspicuous because of the large, circular emergence holes on the dorsum.

According to Silvestri (1919*b*), *B. fasciatus* Foerst. is a common enemy of *Eulecanium coryli* L. in southern Europe, where a maximum parasitization of 50 per cent of the scales has been observed. Oviposition takes place mainly during April; at this time, a considerable number of eggs are present beneath the host scales and the beetle egg is presumably placed among them. The female beetle feeds extensively upon the

[1] According to L. L. Buchanan, the two species here discussed are unquestionably congeneric, though *B. fasciatus* has heretofore been erroneously assigned to the genus *Anthribus*.

body fluids of the host scales and also upon the eggs. The larvae are restricted entirely to the cavity beneath the individual host scale and are dependent upon the eggs found there for food. Thus the relationship is identical with that of the chalcidoid *Scutellista cyanea* Motsch. and its host *Saissetia oleae* Bern. The larva is distinctly weevil-like and very robust, and the legs are represented merely by small conical protuberances. The cycle from egg to adult is complete in slightly less than two months. The adults appear in June and persist without oviposition until hosts of the proper stage become available the following spring. *B. nebulosus* Foerst. is also an enemy of several other species of lecaniine Coccidae in Europe (Prell, 1925).

Neither of the above authors observed actual oviposition, though Yano assumed that the eggs were placed upon or in the vicinity of the host scales and that the young larvae later penetrated into the egg chamber, and Silvestri believed that they were inserted beneath the margin of the scale and into the chamber by means of the extensible ovipositor. Clausen (unpublished notes) has observed oviposition of *B. niveovariegatus*, in both the field and laboratory, in *E. pela* and several species of *Kermes*. As in many other parasitic and predaceous insects, the feeding habit of the female was found to have an intimate relationship with oviposition. The female was noted to break the hardened integument of the host scale and to feed upon the body contents, after which she reversed her position, thrust the ovipositor into the wound and through the thin ventral body wall, and placed the egg within the egg chamber. The beetle egg is usually found adhering to the body wall of the host at the point of penetration of the beetle's ovipositor. Although the feeding wound is quite large, it often heals over and normal oviposition by the scale is then completed, though a considerable number die owing to the injuries received.

The young beetle larvae feed solely upon the eggs; but later, after the death of the host female, they feed extensively upon the body tissues, also. In the case of hosts killed by injury incident to the feeding of the beetle female, the larva may develop largely as a scavenger rather than as an egg predator.

Even in the larger coccid hosts, such as *E. pela* and *Kermes vastus* Kuw., only a single *B. niveovariegatus* develops in each, though the egg supply is adequate to bring several to maturity. As a result, the degree of control exercised is not nearly so high as the 50 to 70 per cent of scales attacked would indicate. In this species, as in *B. fasciatus*, there is apparently only a single generation each year, at least upon the above single-brooded hosts, and the adults emerge in late June, persist in that stage through the winter, and appear for oviposition the following April and May.

MISCELLANEOUS FAMILIES

The information regarding the food habits of the Clavigeridae, Brentidae, Pselaphidae, Leptinidae, and Paussidae is exceedingly limited. Many of them are associated in varying capacities with ants, some are definitely known to be predaceous upon the ant broods, and others are principally scavengers. Park (1929) considers that *Leptinus testaceus* Muell., and possibly the family Leptinidae as a whole, exhibit a facultative parasitism. Some Brentidae and Cryptophagidae are found in bark and wood under circumstances indicating that they are predaceous upon other insects occupying the same habitat.

HEMIPTERA

The Hemiptera are predominantly phytophagous in habit; but a considerable number of species in the more important families have shown a strong tendency toward entomophagy, and in a number of instances of independent origin this has reached the point where plant feeding has been abandoned entirely and the predatory role is now obligatory. This occurs among both the aquatic and terrestrial groups. Although these species show certain preferences in their choice of food, yet the records available indicate that the majority are almost omnivorous.

Extended accounts of the life histories and habits of many British species, as well as descriptions of the immature stages, are given by Butler (1923). These include all the predaceous groups here discussed as well as the strictly phytophagous representatives of the order.

Elson (1937) has made a comparative study of the anatomy of the order in an attempt to correlate structure with food habits. He finds that the predatory forms have developed both external and internal modifications as a result of their change in habit. The front legs are often adapted for capturing and holding the prey. The rostrum is usually short and stout, either straight or curved but never angular, and capable of movement in all directions. The alimentary tract is longer than in other forms, and the salivary glands produce an alkaline secretion which is injected into the body of the host and acts as a poisoning or paralyzing agent. Feeding by the predaceous nymphs and adults usually takes place with the rostrum held in the horizontal plane of the body, whereas in the strictly phytophagous forms it is held at right angles to that plane.

PENTATOMIDAE

The Pentatomidae, so-called because of their five-jointed antennae, are mainly phytophagous, but the subfamily Asopinae has developed the predatory habit to a considerable degree, and a few species have reached the status of obligate predators. Among the latter may be mentioned particularly *Podisus maculiventris* Say of North America, which feeds mainly upon hairless lepidopterous larvae but also attacks those of the Chrysomelidae. It has been referred to as the most useful of the American predaceous Hemiptera and is said to rank next to *Calosoma* as an enemy of the fall armyworm. One individual is recorded to have consumed a total of 122 third- and fourth-instar larvae of *Laphygma exigua* Hbn. during a period of nine weeks. The first-instar nymphs cluster

about the eggshells for several days after hatching and undergo the first molt before any feeding takes place. There are some indications, however, that these young nymphs feed to a limited extent on plant juices, and this habit is shared with many other species that are strictly predaceous after the first molt. There are two generations each year, making the various instars available for attack upon crop pests during practically the entire season, and the winter is passed in the adult stage. The eggs are laid in batches of 20 to 30, and each female is capable of depositing up to 1,000 or more during a period of 5 to 8 weeks. Couturier (1938) has presented an extended account of the biology and habits of this species as a predator of the Colorado potato beetle, *Leptinotarsa decemlineata* Say. It was introduced into France from North America from

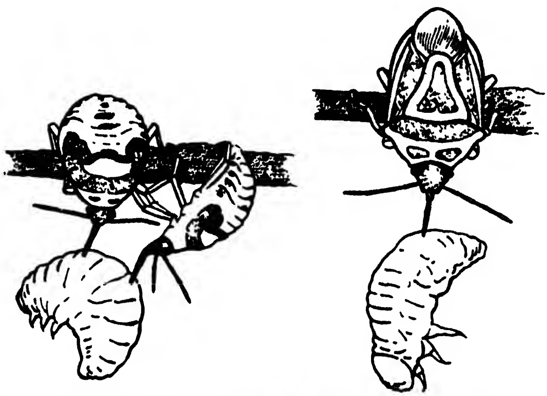


FIG. 248.—Nymphs and an adult of *Perillus bioculatus* F. feeding upon larvae of the Colorado potato beetle. (*From Trouvelot*, 1931.)

1930 to 1933 to aid in the control of this pest, which has become destructive and widely distributed since its first appearance in Europe about twenty years ago.

Podisus serviventris Uhler is predaceous upon a wide range of caterpillars, and its feeding habits are similar to those given above (Preble, 1933). The first-instar nymphs feed upon unhatched eggs of their own kind and upon plant juices, which are essential at this time, and they consistently refuse to attack caterpillars. Plant food may also be taken after the first molt, but the nymphs are unable to develop to maturity without animal food. *P. sagitta* F. is one of the most abundant of the predators attacking *Epilachna* larvae in Mexico.

Perillus bioculatus F. is another North American member of the family that is being utilized against the Colorado potato beetle in France; its habits have been studied by Trouvelot (1932). Both the adults and nymphs attack the beetle larvae, impaling them with their beaks and often holding them suspended in the air while the body fluids are being

withdrawn. The first-instar nymphs feed only upon the eggs and young larvae. It is estimated that each individual destroys 150 to 200 larvae during its lifetime. Landis (1937) found that the eggs constituted the principal food during the nymphal period and that an average of 452 eggs are consumed during the developmental period. In the American localities where this species is abundant, it has been noted that control is quite effective and other measures are not necessary. Several generations are produced each year, and the winter is passed in the adult stage. The females deposit a maximum of about 260 eggs.

Picromerus bidens L. of Europe is known to feed upon the larvae of various Lepidoptera, foliage-feeding Hymenoptera, Chrysomelidae, etc., and is an important controlling factor in relation to several crop pests. Its preference for bedbugs, *Cimex lectularius* L., is of particular interest, and as early as 1776 its use was recommended for the biological control of this pest. A few specimens confined in a heavily infested room were said to have completely exterminated them within a few weeks.

LYGAEIDAE

This family, which includes a number of major crop pests, also has a considerable number of species that derive a part of their food requirements from the body juices of other insects. The subfamily Rhyparochrominae is thought to be mainly predaceous.

The adults and nymphs of *Geocoris punctipes* Say are common predators on the European red mite, *Paratetranychus pilosus* C. & F., on cotton in the southern United States (McGregor and McDonough, 1917). The nymphs consume an average of about 1,600 red spiders during their developmental period, and the adults account for about 80 per day. The eggs are deposited singly among the hosts, and the cycle from egg to adult is complete in about 30 days.

In Fiji, *Germalus pacificus* Banks is considered to be the most important of the natural enemies of the fruit fly, *Chaetodacus passiflorae* Frogg. The nymphs and adults suck out the contents of the eggs, which are embedded in the rind of the fruit.

NABIDAE

The members of this family are generally of predaceous habit. They usually frequent low-growing plants, such as grasses and vegetables, and feed upon the various soft-bodied insects occurring upon the foliage and flowers. The principal hosts are aphids, leaf hoppers, and chermids, but in some species lepidopterous eggs and larvae are included in the fare. The victims are seized with the forelegs, and the beak is inserted at one of the sutures. *Nabis ferus* L., which is well-known in North America as an enemy of the potato psyllid, the sugar-beet leaf hopper, and the

meadow plant bug, is recorded as feeding upon the larvae of *Ascia rapae* L. in Europe. The larger caterpillars are attacked only at the time of the molt. Complete paralysis ensues quickly after penetration of the beak of the bug into the body, and death occurs within 24 hours, even if no feeding takes place. Mundinger (1922) gives an extended account of the life histories and habits of *N. roseipennis* Reut. and *N. rufusculus* Reut.

MIRIDAE

A considerable number of species of the family are known to be of predaceous habit; in fact, several authors state that the family as a whole subsists principally upon other insects. The genus *Deraeocoris* is consistently associated with aphids, being predaceous mainly upon those species which have a waxy covering, such as *Eriosoma* and *Phylloxera*. *D. flavilinea* Costa of Europe has a wide range of food sources, being predaceous upon the eggs and young nymphs of several species of Pentatomidae and upon aphids, syrphid larvae, etc. From 10 to 15 per cent of the eggs of the pentatomid species found upon hazel nuts in Italy are destroyed by this bug (Boselli, 1932). In addition, it feeds upon plant juices. Other species of the family are known to attack red mites, chermids, etc.

One species of the family that is well-known because of its role as a predator is *Cyrtorhinus mundulus* Bredd., which was introduced into Hawaii from Australia and Fiji in 1920 for the control of the sugarcane leaf hopper (Swezey, 1936). It feeds solely upon the eggs and was so effective as quickly to reduce the infestation to a noneconomic level and considerably below that attained through the earlier introduction of the parasitic enemies of the pest. It is quite closely associated with cane and for this reason has not been effective against leaf hoppers on corn. Its eggs are deposited singly or in small groups in crevices in the leaves of cane. More recently, *C. fulvus*, imported from the Philippine Islands from 1937 to 1938, has effectively controlled the taro leaf hopper, *Megamelus proserpina* Kirk., in Hawaii. Both these species are obligate egg predators and are not known to partake of plant food.

ANTHOCORIDAE

Detailed information on the predaceous habits of the flower bugs is limited largely to a considerable number of records regarding *Orius* (*Triphleps*) *insidiosus* Say in North America. Barber (1936) has given an extensive account of the habits of this species, particularly in its relation to the insect pests of corn. The bulk of the records on feeding refer to Thysanoptera and Homoptera, with a lesser number on Hemiptera, Lepidoptera, and Acarina. It is considered to be the most important of the natural enemies of the corn ear worm, *Heliothis obsoleta* F., in

certain parts of the United States. Records taken in Virginia show that the proportion of eggs destroyed ranges from 14 to 54 per cent during the season. The young larvae are also attacked, though to a lesser extent.

O. insidiosus is also the most effective natural enemy of a number of species of thrips attacking truck crops and fruit trees, and this is also true in relation to the European red mite and other mites upon various crops. Feeding experiments by McGregor and McDonough (1917) indicate that

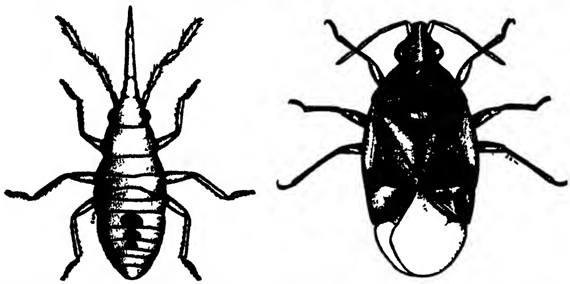


FIG. 249.—A young nymph and an adult of *Orius insidiosus* Say, an efficient predator upon red mites. (*From McGregor*, 1912.)

a nymph consumes an average of about 33 mites per day and the adults a slightly smaller number. Mite eggs are attacked only when the young and adults become scarce. Extensive feeding was noted to occur on the winter eggs of the European red mite during late summer.

Several species of *Acanthocoris* are recorded by Butler as feeding upon aphids in the British Isles; *A. nemoralis* F. has the unusual habit of attacking leaf-mining larvae of the lepidopterous genus *Lithocolletis*.

REDUVIIDAE

The assassin bugs that constitute this family are mainly, if not entirely, insect-feeding in habit and attack a wide variety of insects that frequent plants. Their prey consists most frequently of aphids, leaf hoppers, and caterpillars. In *Amalus* sp. and *Beharus lunatus* L. & S., the fore tibiae and the reduced tarsi are covered with fresh resin, by which means the prey, consisting mostly of ants of the genus *Dolichoderus*, is captured (China, 1932). A remarkable observation has been made by E. E. Green in Ceylon upon the habits of *Physorhynchus linnaei* Stal. The apterous females, which are only ⅙ in. long, attack the giant millepede. This host, which is nearly 6 in. long, is completely and permanently paralyzed, and the beak is inserted for feeding into the ventral area near the caudal end of the body. The Australian *Pristhesancus papuensis* Stal, which is an important enemy of various plant bugs, is recorded as occasionally attacking honeybees.

All the active stages of *Zellus peregrinus* Kirk. are predaceous in habit and subsist in large part upon aphids in fruit trees and leaf hoppers in cane

fields (Swezey, 1905). They are not entirely beneficial, however, as extensive attack upon coccinellid larvae has been frequently observed.

Plank (1939) found nymphs and adults of *Peregrinator biannulipes* Montr. associated with powder-post beetles, *Dinoderus minutus* F., in bamboo in Puerto Rico. Both nymphs and adults attack the beetles upon their emergence from the galleries.

MISCELLANEOUS FAMILIES

The Phymatidae and Enicocephalidae are relatively small groups which inhabit foliage and flowers and feed upon a variety of insects that frequent them.

The members of the superfamily Gerroidea are predominantly aquatic in habit and the nymphs and adults of the Gerridae, Vellidae, Naucoridae, Nepidae, Belostomatidae, and Notonectidae feed principally upon insects and a variety of the smaller animal life found in the ponds and streams that they inhabit. Some of the larger forms even prey upon tadpoles and small fish. The Ochteridae and Nerthridae are of littoral habit and are predaceous upon such insects and other small animals as frequent the muddy margins of ponds and streams.

THYSANOPTERA

The predaceous habit is well-developed in a number of species of the order, and at one time the entire group was considered to be essentially predaceous rather than phytophagous. It has now been established, however, that although the latter is the predominant habit some species partake of both types of food and still others subsist solely on insect food. *Scolothrips sexmaculatus* Perg. is recorded from many parts of North America as feeding upon various species of red mites. The eggs are preferred, though nymphs and adults are also attacked. The species also has been observed to attack the citrus thrips extensively, and this tendency to prey upon members of its own order has been noted in several other instances. C. V. Riley records an undetermined species as being very effective in destroying the eggs of the plum curculio. There is evidence to indicate that members of the order may be of some importance as predators upon lepidopterous eggs, particularly those of small size which have a membranous chorion. *Aleurodothrips fasciapennis* Frankl. is an important enemy of the citrus white fly, *Dialeurodes citri* Ashm., in Florida. Both nymphs and adults feed extensively upon *Aspidiotus destructor* Sign. in various parts of the world (Taylor, 1930). The eggs are laid in empty puparia or beneath scale covers and at times in scales from which parasites have emerged.

TRICHOPTERA

The larvae of the caddis flies are all aquatic in habit and feed mainly upon decaying vegetation in the water, though some species are predaceous. The eggs are laid in masses either upon stones, plants, or other objects in the water or upon objects above the water surface. The larvae are eruciform and build about themselves silken cases or tubes which are overlaid with particles of sand, small pebbles, or other objects.

MECOPTERA

The order is a small one consisting of the so-called scorpion flies, of which the adults of most species are distinguished by the prolongation of the front of the head into a distinct beak. Some species are wingless. The adults are mainly predaceous upon other insects, principally Diptera.

The larvae are eruciform and are found on or in the soil in rather damp places. Those of *Panorpa* feed upon dead or dying insects and rarely if ever upon active living forms, and *Bittacus* is essentially predaceous upon such insects and other small animals as are present in or on the moist soil.

PLECOPTERA

The stone flies inhabit pure and well-aerated waters and consequently are found only in brooks and streams and on lake shores. The nymphs of the majority of species feed upon aquatic vegetation, and only in the Perlidae, particularly the genera *Perla* and *Acroneuria*, are they essentially carnivorous. In this family, the mouth parts of the nymphs are definitely modified as a consequence of this habit. On the basis of the more recent classification proposed by Frison (1935), the predaceous species are contained in the families Perlidae, Perlodidae, and Chloroperlidae. The last family shows a wide range in food habits.

NEUROPTERA

The several families of the order are predominantly predaceous in habit, the larvae being quite generally so and the adults likewise, if they feed at all. From the economic point of view, the Chrysopidae and Hemerobiidae are of greatest importance owing to their attack upon aphids, scale insects, etc. Killington (1936) gives an extended review of the food sources of the larvae of the order. With the exception of the Osmylidae and Sisyridae, the prey of the adults is the same as that of the larvae. There is a wide range in habitat occupied by the larvae; some (Myrmeleontidae, Nemopteridae, Ascalaphidae, Nymphidae) are found only in sand or dust, others are arboreal (Chrysopidae, Hemerobiidae, Coniopterygidae, Psychopsidae), and several are aquatic or semiaquatic (Sialidae, Sisyridae, Osmylidae).

A general summary of the characters and habits of the order has been given by Withycombe (1923, '24*b*), and Rabaud (1927) presents a comparative study of the larval forms and habits of representatives of a number of families. The most complete information of the immature stages and the biology of the different families is found in the recent publications of Killington (1936, '37).

The eggs of all families are oval in form, at times somewhat flattened, and have a distinct micropylar structure. In the Mantispidae, the majority of Chrysopidae, and some Berothidae, they are borne at the end of slender stalks. Hatching is effected by the use of a saw-like egg breaker, the form and functioning of which are described by R. C. Smith (1922*a*). This structure is a part of the presumed amnion which surrounds the embryo, lying over the head on the median line, and is discarded when the body is only partly out of the shell. This is termed a "prelarval" skin by some authors.

The larvae of practically all families are carabiform and with few exceptions possess very large, curved mandibles, by means of which the body of the prey is pierced and the fluids sucked out. The occurrence of three larval instars appears to be quite general throughout the order, though there are several apparent exceptions. The mouth is closed by a membrane only in the first instar. The cocoons are spun from a silken thread given off from the tip of the abdomen. Pupation without a cocoon has been noted only in the Raphidiidae and in occasional individuals of some species of Chrysopidae. The pupa lies immobile in the cocoon until a short time before the end of the stage; at this time, it

becomes active, emerges from the cocoon, and then transforms to the adult. There is some disagreement among authors as to the manner of emergence from the cocoon. Some assert that the mandibles of the pupa are used in cutting away the circular cap, whereas others believe that this cap is built into the cocoon by the larva and that it is either pushed off or dissolved away by the active pupa. In the Chrysopidae, it has been noted that the pupa is able to inflate its body very appreciably; this would aid greatly if the cap is to be removed by pressure alone.

No excrement is passed during the larval period, and without exception the meconium is cast by the adult insect rather than by the prepupa or pupa. It is in the form of a dark pellet enveloped by the peritrophic membrane. The failure to void excrement during the larval period is a consequence of the type of food consumed. All predaceous species suck out the body fluids of the host, and such food material contains a minimum of solids that cannot be utilized.

SIALIDAE

This is a small family, represented by only a few species. The larvae of *Sialis* and several other genera are strictly aquatic in habit and are presumed to feed, in part at least, upon other aquatic insects and the smaller animal life present in the water that they inhabit. The eggs are deposited in large masses on vegetation over or near water.

RAPHIDIIDAE

Information regarding the feeding habits of the snake-flies, which constitute this family, and their larvae is limited to incomplete observations on a relatively few species, largely the genus *Raphidia*. Carpenter (1936) reviews the published information regarding the habits of the family, practically all of which relates to European species.

In captivity, the adults of *Raphidia notata* F. were found to feed readily upon aphids but upon larger insects, such as flies and beetles larvae, only after they had been injured and were consequently unable to escape or to defend themselves. Those of *Agulla unicolor* Carp. fed freely upon freshly killed Chironomidae. They exhibit a pronounced cannibalistic tendency. The eggs of this family are usually deposited in clusters in crevices in the bark of trees. The larvae are found under bark, though they also inhabit decaying wood, etc. They prey principally upon aphids, caterpillars, and other soft-bodied insects. Pupation takes place in an oval cell beneath the bark or in decayed wood. The life cycle apparently covers several years.

An undetermined species of *Raphidia* was introduced into New Zealand from California in 1890 for the control of the codling moth, but establishment was not effected.

ITHONIDAE

The only observations upon the biology and habits of a member of this family relate to the Australian *Ithone fusca* Newm., which is said to be predaceous upon various soft-bodied insects, particularly scarabaeid larvae, that inhabit sandy soil (Tillyard, 1922). More recent investigations have shown that the larvae are unable to feed upon other insects and probably derive their food from plant roots.

HEMEROBIIDAE

The adults of the brown lacewings are, as the name indicates, brown in color and thus may be readily distinguished from the bright-green Chrysopidae, which are found in the same environment. All species are predaceous and attack principally aphids, but also chermids, mealybugs, white flies, and occasionally diaspine scale insects. Several species are restricted largely to a certain type of tree and consequently feed only upon such insects as live upon these trees. Observations upon the habits of a number of species of the genus *Hemerobius* have been recorded by Withycombe (1922, '23). *H. pygmaeus* Ramb. is confined solely to oak, whereas *H. atrifrons* McL. and *H. pini* Steph., according to Killington (1932), are found only upon conifers. The latter author (1936, '37) has presented detailed information regarding the immature forms and habits of a number of species.

Several efforts have been made to utilize the brown lacewings in biological control projects, and Bodenheimer (1928) asserts that effective control of *Pseudococcus citri* Risso was secured in Palestine through the liberation of large numbers of the native *Sympherobius amicus* Nav. Several species of *Hemerobius* have been introduced into Canada, Australia, and New Zealand for the control of Chermidae attacking forest trees.

Withycombe states that the eggs in all species are laid on the side. They are whitish, grayish, or even pink in color and elongate-oval, with the chorion often pitted, and bear a knob-like or disk-like micropyle, often of considerable size. In *Wesmaelius*, the chorion is densely studded with glossy papillate projections. The egg breaker is saw-shaped. The eggs of *H. pini* are pale cream color, changing to brown before hatching.

There are three active larval instars, which are quite similar to the larvae of the Chrysopidae. Only the first-instar larva has the trumpet-shaped tarsal claws, whereas they occur on all instars of the above family. No species is known to carry a trash packet upon the dorsum of the body, and consequently none has the hooked setae.

The cocoons of the Hemerobiidae differ markedly from the nearly spherical parchment-like ones of the Chrysopidae, being loosely woven,

double-walled, and elliptical in outline. They are usually found in protected places rather than exposed upon the foliage or bark. The pupal skin is cast outside the cocoon.

Several generations are usually produced each year, the number depending on climatic conditions. *S. amicus* has eight generations in Palestine, with the minimum life cycle requiring only 23.5 days. *H. pygmaeus* and several others have only a single annual generation in England. The average duration of the egg, larval, and cocoon stages under summer conditions in temperate regions is about 5 to 12, 10 to 18, and 12 to 16 days, respectively. The majority of species hibernate as either larvae or pupae within the cocoons, though *H. stigma* Steph. may be found in the adult form during the winter and *H. pygmaeus* occurs only as a free larva in sheltered places. *Wesmaelius concinnus* Steph., however, hibernates in the egg in England, and this stage persists for a period of seven months.

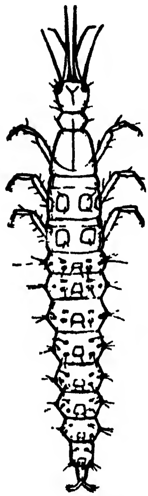


FIG. 250.—A larva of *Euosmylus stellae* McL. (*From Tillyard, 1926, by permission of Angus & Robertson, Ltd., Sydney.*)

Withycombe has called attention to the occurrence of two color forms of adults in many species. The normal summer form is brown, whereas that found during the winter is grayish-brown and spotted.

The full reproductive capacity is known only for *S. amicus*, for which Bodenheimer records an average production of 250 eggs by a series of females and a maximum of 589 by one individual. R. C. Smith (1923) has studied the habits of a series of North American species and found that the gestation period covers about five days. A maximum production of 460 eggs was secured from *Hemerobius humuli* L., though this was from a field-collected female and may not represent the total capacity. *Micromus posticus* Wlk. deposits up to 58 eggs per day. From the above, it would appear that egg deposition in the family may be somewhat higher than in the Chrysopidae.

OSMYLIDAE

The family is represented by only a few species, the adults of which are of relatively small size. The best known is *Osmylus fulvicephalus* Scop. This has been studied by a number of early authors, and more detailed accounts are given by Withycombe (1923) and Killington (1936). The larvae are amphibious in habit and probe into the mud with their long, slender mandibles for the larvae of *Chironomus* and other Diptera inhabiting the wet, mossy borders of streams and similar places. The eggs are elongate-oval and somewhat flattened, with the chorion bearing reticulate

markings, and the micropyle is knob-like. They are deposited in rows upon some object near the water's edge. Hatching takes place in about 22 days, and larval maturity is attained the following spring. The cocoon is spun in damp moss, and the adult emerges 10 to 12 days later.

SISYRIDAE

The family comprises only a few genera and species. The larvae of *Sisyra fuscata* F. are entirely aquatic in habit and suck out the body fluids of fresh-water sponges. These larvae are distinguished by the possession of paired, jointed gills on the venter of the first seven abdominal segments. The eggs are deposited in clusters, covered with a web of white silk, upon foliage or other objects overhanging water.

PSYCHOPSIDAE

Very little is known regarding the biology and habits of this family. Tillyard (1918) has given an account of *Psychopsis elegans* Guer., the larvae of which are predaceous upon various insects that frequent the trunks and branches of *Eucalyptus* and related trees. The oval eggs are deposited in small groups upon the bark during midsummer. Larval feeding takes place at rather long intervals, and as a consequence the period of development extends over two seasons. Incubation of the egg requires 12 days, and hibernation takes place as a first-instar larva. The second winter is passed in the third larval stage after feeding is completed. The cocoons, which greatly resemble those of *Chrysopa*, are found in crevices in the bark. The cocoon stage is complete in three weeks.

CHRYSOPIDAE

The green lacewings that comprise this family are the most commonly encountered of all the predaceous Neuroptera of arboreal habit. Their large size and bright coloring, often with golden eyes, make the adults very conspicuous. The larvae, commonly termed aphis lions, are distinguished in some species by their habit of carrying a packet of trash over the dorsum, which is renewed after each molt. The cocoons are usually white, parchment-like in texture, and nearly spherical. The eggs of the great majority of species are borne at the ends of stalks of varying length, and they are deposited upon the foliage of plants upon which the host insects are feeding.

The food of the family consists of a variety of soft-bodied insects, but more particularly the aphids and mealybugs. Leaf hoppers, thrips, lecaniine Coccidae, mites, etc., may also be attacked. Extensive feeding takes place at times upon the eggs of various Lepidoptera. The larvae of *Chrysopa rufilabris* Burm. have been noted to pierce leaf tissue with the mandibles in order to feed upon larvae of *Agromyza jucunda* v.d.W. in

their mines. This species is an important predator upon red mites on cotton; the larvae are said to consume an average of 80 per day during the entire developmental period. In general, the adults feed upon the same insects that serve as prey for the larvae, though their activities in this respect are not nearly so great. The more extended accounts of the biology and habits of members of the family are by Wildermuth (1916), Smith (1921, '22*b*), and Withycombe (1923).

A number of species of *Chrysopa* have been introduced into New Zealand for use in the control of aphid and mealybug pests and also against Chermidae attacking pine.

Adult life usually extends over a period of four to six weeks. Oviposition may take place the day following emergence from the coccoon and mating, though occasional species pass the winter as adults and oviposit

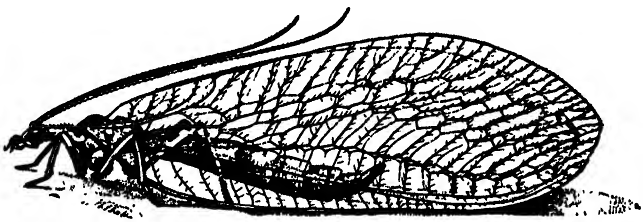


FIG. 251.—The adult female of *Chrysopa californica* Coq. (*From Wildermuth*, 1916.)

the following spring and summer. It is stated by Withycombe that no spermatophore is produced at mating, though Killington (1935) refers to one carried by a female of *Nathanica fulviceps* Steph. The number of eggs deposited by the different species is variable and the maximum recorded by Smith is 617 by a female of *Chrysopa occulata* Fitch in 42 days. This, however, is believed to be exceptional, and the general average is probably between 100 and 200. Killington (1936) cites oviposition records secured by various workers, among which are those by Okamoto of 550 eggs from *C. nipponensis* Okam. and by Withycombe of 480 eggs from a female of *C. phyllochroma* Wesm.

Although the eggs of all species are of similar form, being oblong in outline, with a small micropylar structure at the anterior end, and are usually borne at the ends of filamentous but rigid stalks, there is considerable variation in the form of the stalk itself and in the position in which it is placed. Smith states that the length of the stalk varies directly with the length of the abdomen of the female. The maximum length attained in the larger species is about 15 mm. A number of species deposit their eggs singly or in small groups on the undersides of leaves, but *C. albolineata* Kill. places them at the edge, with the stalks in the same plane as the leaf. According to Withycombe, *C. flava* Scop. and *C. flavifrons* Brauer have the unusual habit of depositing the cluster of eggs, numbering up to 40,

on a common stalk, from the tip of which they radiate brush-like. This stalk represents, in reality, a number of individual stalks which have fused. In *Notochrysa capitata* F. the eggs are placed radially upon pine needles, and the stalks are knotted at regular intervals, or moniliform. The provision of a stalk on which the eggs are borne is believed to be for protection against enemies. This, however, is not entirely successful, for it has been noted that newly hatched larvae frequently feed upon the eggs that are still unhatched, and they are known to be parasitized by several species of Scelionidae. Williams (1931) states that the numerous species of *Anomalochrysa*, native to the Hawaiian Islands, have elongate-oval eggs which are deposited upon the foliage and lack the stalk entirely.

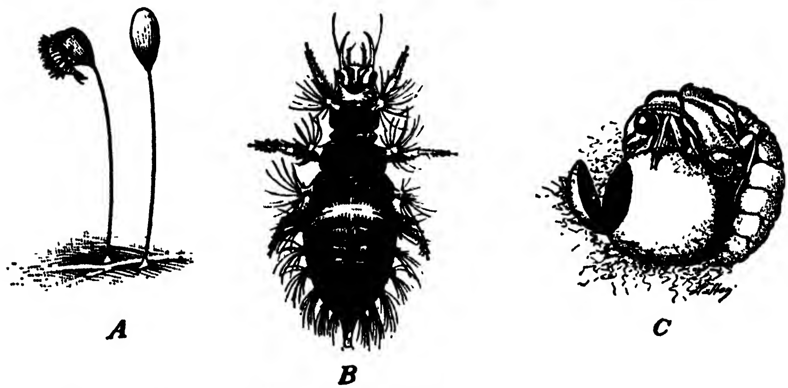


FIG. 252.—Immature stages of the Chrysopidae. *A* and *B*, the eggs and a mature larva of *Chrysopa microphya* MacL. (*from Terry*, 1905); *C*, a pupa of *C. californica* Coq. after emergence from the cocoon (*from Wildermuth*, 1916).

In color, the eggs are white or pale yellowish-green at the time of deposition but change to bluish-green and finally to gray before hatching.

Jacobson (1912) mentions that the newly hatched larvae of *C. jacobsoni* v.d.W. return to the egg cluster during the first two nights after hatching and remain head downward upon the stalks.

There are three larval instars, which do not differ in their essential characters. Each has a rather elongate body, with nine abdominal segments, and is clothed with hairs which, in the trash-carrying species, are hooked at the apex. The head is flat, and the enormous sickle-like jaws and the maxillae extend directly forward. The mandible and maxilla on each side are held together by a flange which fits into a groove, and they thus form a sucking tube through which the body fluids of the host are drawn. The true mouth is stated to be completely closed.

The habit of carrying a packet of trash dorsally over the body serves as a ready means of distinguishing the larvae of certain species of the family from those of the Hemerobiidae. These larvae have the abdomen conspicuously arched and shortened. The packet is rebuilt after each

molt. Various materials, such as host remains and debris, are used in its construction. Smith describes the formation of the packet in *C. lineaticollis* Fitch and states that the larva first thrusts its head beneath the bit of debris and then utilizes the jaws in working it backward to the thorax. The numerous fragments are more or less woven together and are forced backward as new additions are made at the front. The anterior half of the packet is free but rests upon the thoracic tubercles. Other authors state that the fragments are thrown backward over the dorsum and are not fastened together. The species that carry the trash packet live almost entirely in the open, and the adaptation is consequently considered to be for protective purposes. When larval maturity is reached, some species seek out protected places for pupation, whereas others spin the cocoon on the flat leaf surface.

The oval, parchment-like cocoon is formed from silken strands produced by modified Malpighian tubes and given off through the anal opening. The hinged lid is merely pushed off by the pupa at the time of emergence rather than being cut with the mandibles. Jacobson (1912) states that this lid is formed by the larva at the time the cocoon is spun, but later authors are uncertain regarding the manner of its formation. The pupa lies curled within the cocoon and becomes active only a short time before the appearance of the adult. It is able to inflate its body to several times the original volume, thus greatly facilitating the opening of the lid of the cocoon, whereupon it crawls out, wanders about somewhat for one or two hours, and then transforms to the adult. Occasional individuals pass through the pupal stage without forming a cocoon. In the case of multibrooded species, it has been observed that overwintering adults are somewhat brownish in color as contrasted with the green of the summer broods, the seasonal change in coloration thus being comparable to that noted in the Hemerobiidae.

The life cycles of the Chrysopidae are directly influenced by climatic conditions, and marked differences occur in the records for the same species under summer conditions in various sections and countries. In general, the development from egg to adult is complete in approximately one month. Wildermuth records the duration of the egg, larval, and cocoon stages of *C. californica* Coq. as 6 to 12, 11 to 22, and 14 to 23 days, respectively. The eggs of *C. rufilabris* hatch in 3–5 days, and the larval and cocoon stages require 18 and 6 days, respectively. Hibernation may take place in any stage except the egg, though the majority pass the winter in the larval or prepupal stage within the cocoon. *C. californica*, *C. carnea* Steph., and *C. ploribunda* Fitch hibernate as adults in protected places. The number of generations per year is variable, ranging from only one for *C. albolineata* in England to at least six for *C. californica* under Arizona conditions.

NEMOPTERIDAE

Only a relatively few species are included in this family, which is closely related morphologically to the Myrmeleontidae. The adults are distinguished by the exceedingly long and narrow hind wings. The larvae show a marked constriction between the head and thorax, which reaches its greatest development in the grotesque *Necrophylus arenarius* Roux, a species that occurs in the tombs of Egypt and under ledges along the Nile. The neck is exceedingly slender and is as long as the remainder

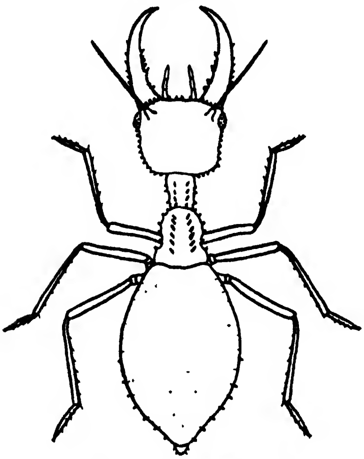


FIG. 253.—The first-instar larva of *Croce filipennis* Westw. (*From Imms*, 1911.)

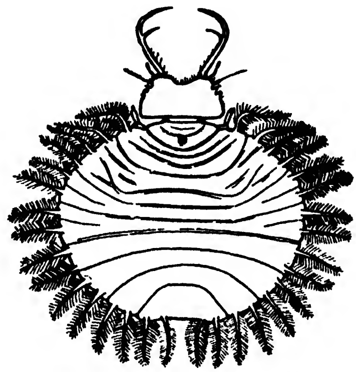


FIG. 254.—A larva of *Osmylops pallidus* Banks. (*From Tillyard*, 1926, *by permission of Angus & Robertson, Ltd., Sydney.*)

of the body. The larvae of all known species live in the dust on the floors of caves, in neglected buildings, and in other sheltered places.

Croce filipennis Westw. (Ghosh, 1910; Imms, 1911) lives in abandoned buildings where the larvae lie in wait on the floor for passing insects, particularly Psocidae and Dermestidae, the former of which is probably the preferred food. The oval eggs as well as the spherical cocoons are also found in the dust on the floor. The life cycle covers one year, of which the egg and pupal stages require 10 to 12 and 18 to 22 days, respectively.

MYIODACTYLIDAE

The family contains only a very few genera and species and is restricted in distribution to the Australian region and to certain South Pacific islands.

The larvae of *Osmylops pallidus* Banks (Fig. 254) are almost circular in outline, with conspicuous mandibles. They lurk upon the undersides of the leaves of eucalyptus trees and prey upon other insects.

NYMPHIDAE

Nymphus myrmeleonides Leach, the only well-known member of the family, is found in Australia and certain islands of the South Pacific. The larvae are found under rubbish, each covered so that only the front of the head and the mandibles are exposed. They probably prey upon wood ants, which are common in the environment that they inhabit. A spherical, parchment-like cocoon is formed.

MYRMELEONTIDAE

This relatively small family comprises the well-known ant lions, so-called in the larval state because of their habit of feeding mainly upon ants and their ferocious appearance and manner of attack. The genus *Myrmeleon* is one of the most highly specialized of the order and, because of its cosmopolitan distribution and abundance, is the dominant group, with the possible exception of the Chrysopidae.

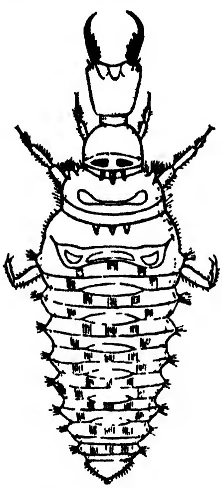


FIG. 255.—A larva of *Acanthaclisis fundata* Wlk. (*From Tillyard, 1926, by permission of Angus & Robertson, Ltd., Sydney.*)

A detailed account of the habits of *M. formicarius* L. was published by Reaumur in 1742, and the information presented has been supplemented by numerous later authors. An extended review of the biology and habits is given by Wheeler (1930). The eggs are small, are oval in outline, and are deposited during the autumn in small groups, adhering end to end, in the sand. Hatching takes place shortly thereafter, and a period of feeding ensues before hibernation. The young ant lion is slender, with conspicuous mandibles and a tough integument, which is essential not only for defense but for protection against desiccation. There are several types of setae on the dorsum of the body which serve to transmit the stimuli from falling sand particles, indicating the presence of a victim in the pit.

The formation of the pit by the larva is of particular interest. It is accomplished only at night and begins with the making of a circular groove in the sand, which indicates the margin of the pit which is to be formed. The larva moves backward, utilizing its head and closed mandibles to throw the sand from the inner border of the groove to the outside. The circle that is followed in this process is gradually narrowed, thus reducing the cone of sand in the center and deepening the furrow. Eventually the pit is completed, and the larva takes its position at the bottom, with the entire body except the mandibles covered with sand.

Here it awaits the coming of a victim, which is seized as soon as it tumbles to the bottom of the pit. If not within reach of the mandibles, it is showered with sand until its struggles bring it nearer. Death takes place very quickly, the body juices are sucked out, and the remains are then tossed or dragged out of the pit.

There are three larval instars, which do not differ appreciably in general characters, though the body becomes more robust as maturity is reached. The developmental period is uncertain and may extend over several years. The larvae are capable of existing for very long periods without food. Maturity is reached in late spring or early summer, and the spherical double-walled cocoon is then spun beneath the sand. Pupation takes place about one week later, and the adult emerges in four to six weeks. The pupa cuts a circular opening in the cocoon wall with its mandibles and comes to the surface of the sand before casting its skin to release the adult.

Gravely and Maulik (1911) observed the habits of *M. contractus* Wlk. in India and found that it departs from the habit of all other members of the genus in not forming pits in sand. Instead, it inhabits the trunks of mango trees coated with dried mud, and the larvae are usually found on the surface or in shallow depressions. The cocoon is spun in a crevice in the bark, and at emergence of the adult the pupal skin is left partly extruded from the opening in the cocoon.

ASCALAPHIDAE

The members of this family have much in common with the Myrmeleontidae, in that the larvae lie in wait for their prey, which consists of a variety of soft-bodied insects. They do not, however, build pits; instead, they utilize natural depressions for concealment and often cover their bodies with dust. Larvae of this group may be distinguished from the true ant lions by their habit of walking forward, rather than backward. The adults have a certain resemblance to dragonflies but may be distinguished by the long, clubbed antennae. They are crepuscular in habit.

McClendon (1902) has given an account of *Ululodes hyalina* Latr., which occurs in the southern United States and Central America. The eggs (Fig. 256) are deposited in groups of 50 to 75 in a double row at the end of a twig, and the mass is fenced off slightly below the base by several circles of "repagula" placed on end. These repagula are considered to be aborted eggs, produced by certain ovarian tubules at the same time that others produce normal eggs. This formation is said to serve as a protection for the egg mass from insect enemies. The incubation period covers 9 to 10 days.

The larvae hide in depressions in the soil or under the edges of stones and cover their bodies with sand or dust. While they are waiting for the approach of a victim, the huge mandibles are held widely separated. The body juices of the victims are absorbed through a duct formed by the fitting together of the curved mandible and the maxilla. There are three larval instars, and development is complete in about 62 days.

Helicomitus dicax Wlk. (Ghosh, 1913) deposits its dark-brown eggs in single rows, each of which contains upward of 40. As in other species of the family, there are three larval instars. The larvae live upon the surface of the ground, beneath a dust covering which conceals all but the mandibles. These are used in placing the particles of dust or sand upon the back, and it is stated that each mandible can be moved independently of the other. The pupa emerges from the cocoon by bursting it rather than by dissolving or cutting away an opening. There is a single generation each year, and the winter is passed in the active larval stage.

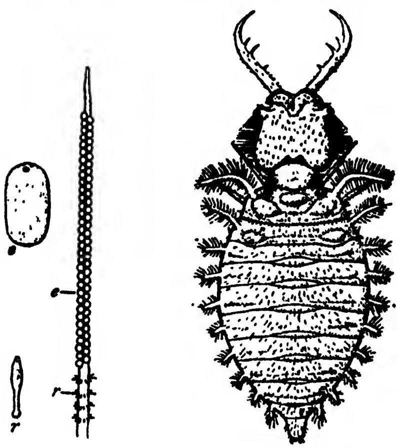


FIG. 256.—The mature larva of *Ululodes hyalina* Latr. and, at left, a group of eggs on a twig, guarded below by rings of repagula. (*From McClendon, 1902.*)

The larvae of *Pseudoptynx* sp., studied by Gravely and Maulik (1911), do not have a covering of sand or rubbish but conceal themselves in depressions in the bark of trees. Here they are very inconspicuous, the legs being hidden and the mandibles so widely separated that they lie along the sides of the head and thorax. The larvae of *Ascalaphus insimulans* Wlk. assemble in linear groups upon plant stems, with their bodies overlapping, so that only the heads and widespread mandibles are visible.

Several species that depend upon protective coloration rather than a soil covering are mentioned by Wheeler (1930). One undetermined species from Panama has a greenish-colored larva that inhabits the leaves of trees and lies with its body flattened along the mid-rib on the upper surface. When it is awaiting the prey, the mandibles are opened so widely that they are completely hidden beneath the lateral margins of the thorax.

MANTISPIDAE

Relatively little is known of the biology and habits of this family. The adults have large raptorial forelegs, somewhat similar to those of

the Mantidae, which are used in capturing other insects. The larvae, so far as known, are predaceous in the egg sacs of spiders. Brauer (1869*b*) gave the first and most complete account of one of these species, *Mantispa styriaca* Poda, which develops in the egg sacs of Lycosidae and related families. This account has been supplemented by the observations of Bristowe (1932). The eggs are stalked like those of the Chrysopidae and are deposited in the autumn in clusters upon the bark of trees, etc., apparently without relation to the host. Hatching takes place about three weeks later, and the young larvae then go into hibernation without any feeding whatever. In the following spring or early summer, when the spider-egg masses have been deposited, they search them out, tear

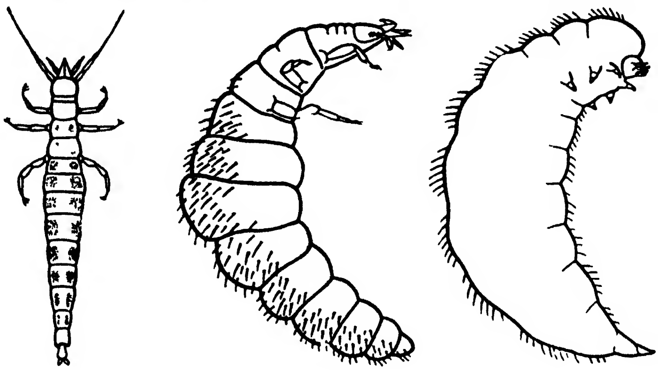


FIG. 257.—*Mantispa styriaca* Poda. *A* and *B*, the newly hatched and fully fed first-instar larvae; *C*, the mature larva. (*Redrawn, after Brauer*, 1869.)

a hole in the covering, and enter. Here they wait for a further period until hatching takes place, whereupon there is extensive and rapid feeding. A molt is said to occur immediately after hatching, and the second one, which is the last, takes place after some feeding. The third-instar larva (Fig. 257*C*) differs greatly from the active second instar; the head is small, the abdomen very large, and the legs rudimentary. It is incapable of ordered movement which, of course, is unnecessary within the confines of the egg sac. The larva completes its feeding, and then spins its yellow, oblong cocoon, in which the pupa is formed, within the unbroken larval skin. In due time, this pupa forces its way out of the old larval skin, cocoon, and host egg sac, wanders about for a time, and finally casts its skin to produce the adult insect.

Observations have been made on several species of *Mantispa* by R. C. Smith (1934). A female of *M. sayi* Banks deposited a total of 2,200 eggs, in six lots, during a period of approximately one month. These were placed in dense clusters and hatched in 9 to 11 days. The young larvae were very active but could not be induced to enter spider-egg sacs or to

feed upon eggs, and all died in a relatively short period. The females of *M. brunnea* Say were found hiding in flowers; in this position they were able to capture readily such other insects as came to the flowers to feed. These females are quite similar in general form and color to *Polistes*. When confined in cages, they lived for about one month and deposited about 250 eggs each. The eggs are elongate-oval and salmon or cream in color and are borne on slender stalks about one and one-half times as long as the egg itself.

Hoffman (1936) mentions that a single female of *Climaciella brunnea* var. *occidentalis* Banks deposited a total of 1,028 eggs, in a single cluster, in one day. They are salmon-colored, and each stands upon an exceedingly slender stalk which is slightly longer than the body of the egg. The incubation period covers 28 days. The young larvae are able to stand erect by the use of the caudal sucker. Some of these larvae were kept alive for four and one-half months without food, which suggests an overwintering habit similar to that of *Mantispa*.

Kishida (1929) describes the finding of as many as eight larvae of *Eumantispa harmandi* Nav. in cocoons of several spiders in Japan. One of these spiders forms its egg sacs in curled leaves of various grasses, whereas another burrows in the soil. There are stated to be only two larval instars, and the last is similar to that described above for *M. styriaca*.

Symphrasis varia Er. has been recorded by Brauer as parasitic in the nests of a wasp in South America, and the cocoon is said to be spun in the cell. Verification is required before this departure from the presumed normal habit of the family can be accepted, particularly as a spider-egg mass may quite possibly have been contained in the nest.

CONIOPTERYGIDAE

No extensive studies have been made upon this group of relatively minute insects. So far as known, the larvae of all species are predaceous, attacking principally red mites, though several species are recorded upon other hosts. *Fontenellea maroccana* Carp. & Lest. attacks *Orthesia* in North Africa, and T. Ishii mentions that the adults of an undetermined species were observed feeding upon *Cryptoparlatoria leucaspis* Lind., on cryptomeria in Japan. Withycombe (1923, '24*a*) has found several species to be predaceous upon *Phylloxera*, and his observations indicate that the feeding range of the various species is quite wide. *Conwentzia psociformis* Curt. is largely associated with oak in England and feeds mainly upon *Phylloxera* but also upon diaspine Coccidae, red mites, etc. (Arrow, 1917). An attempt was made in 1924 to establish this species in New Zealand, but without success.

The eggs are deposited singly upon infested foliage. They are oval in outline, flattened dorsoventrally, and slightly pointed at the micropylar end. The surface of the chorion bears reticulate markings. The eggs of *C. hageni* Banks are yellowish-pink in color, though some may have an orange tint (Quayle, 1913). *C. psociformis* deposits a total of approximately 200 eggs.

The number of larval instars is uncertain, though Quayle mentions four for *C. hageni*. The larvae of this species feed upon all stages of red mites, and the body contents are entirely sucked out from a single puncture. One larva consumed a total of 226 red mites during its feeding period. The oval, somewhat flattened cocoons of *Conwentzia* are usually found on the undersides of leaves or on the bark and are composed of a double layer of silk, with the margins loosely woven. That of *Semidalis aleyrodiformis* Steph. is not strictly double. Withycombe states that the pupal skin is often left within the cocoon rather than discarded after emergence of the pupa.

The life cycle of *C. hageni* is complete in 37 to 43 days under summer conditions, of which the egg, larval, and cocoon stages cover 6 to 8, 18 to 22 and 13 days, respectively. *S. aleyrodiformis* passes the winter in the mature larval stage within the cocoon, whereas a portion of the adults of the first brood of *C. psociformis* persist in sheltered places until the following spring.

ODONATA

The dragonflies and damsel flies number several thousand species, the great majority of which are found in tropical and subtropical regions. All species are predaceous in both the nymphal and adult stages. The nymphs, which are practically all of aquatic habit, feed upon a wide variety of animal life, including crustaceans, tadpoles, small fish, and many water-inhabiting insects. The adults capture their insect prey while in flight. The smaller species confine themselves largely to mosquitoes and other flies of similar size, whereas those of greater size are able to capture the largest Diptera, etc. Members of that order and of Lepidoptera and Hymenoptera constitute the bulk of the prey. *Mesothemis simplicicollis* Say is recorded as feeding very extensively upon adult Tabanidae in Louisiana, and *Cacergates leucostica* Burm. and others of that genus are effective predators upon the tsetse fly in Africa, being credited with effecting a marked reduction in its population. As a whole, the order is markedly beneficial, except for a few isolated instances such as that recorded in Russia, where *Aeshna cyanea* Mull. destroyed nearly half the honeybee population in certain sections. This occurred at the time of extended migrations and is attributed to a lack of the normal food supply. The American *Coryphaeschna ingens* Ramb. may likewise cause serious losses to beekeepers.

Lestes temporalis Selys is said 'to be injurious to various deciduous fruit trees in Northern Japan because of its habit of making oviposition incisions in the young shoots during July and August. Only those trees situated near water are subject to this injury.

The eggs of other species are usually deposited in incisions in stems of plants below the water surface, in muck, or in rotting logs or they may be placed directly in the water while the females are in flight. The metamorphosis is simple; and the nymphs, when mature, crawl out of the water onto rocks, plants, etc., and the adults then emerge.

CORRODENTIA

According to Pearman (1932), several species of psocids are predaceous upon Coccidae, particularly the mealybugs. They feed also upon various insect eggs and possibly upon small aphids. Some authors, however, have asserted that their food consists largely of the wax secretions of the scale insects rather than the body contents.

ORTHOPTERA

The Orthoptera in general are not highly specialized in their food habits. Though a considerable number of species have been noted to prey upon other insects, yet only in the Mantidae has this habit been shown to be obligatory. There is a pronounced tendency toward cannibalism in many families, and the animal food supplements that derived from the more normal sources.

TETTIGONIIDAE

The long-horned grasshoppers include a number of species of predaceous habit. *Conocephalus saltator* Sauss. (*Xiphidium varipenne* Swezey), which feeds mainly upon insects, is recorded from Hawaii as an enemy of leaf hoppers and various other insects inhabiting cane fields and has been credited with being the principal factor in the natural control of mealybugs (Swezey, 1905; Illingworth, 1929). *Clonia vittata* Thbg. of South Africa appears to limit itself largely, if not entirely, to an insect diet, which consists principally of the caterpillars of *Busseola fusca* Hamp. but includes also various grasshoppers and locusts.

GRYLLACRIDAE

According to R. C. Smith (1920), the adults of *Udeopsylla robusta* Hald, occur very abundantly at lights during the summer, when they feed very extensively upon *Lachnosterna* beetles attracted to the same vicinity. The legs of the beetles are usually gnawed off. They also feed readily upon various grasshoppers.

GRYLLIDAE

A number of species of *Oecanthus* show pronounced entomophagous tendencies, and some apparently thrive upon a diet of insect food only. Aphids and scale insects are most frequently attacked by the tree-inhabiting forms. One fourth-instar nymph of an undetermined species is recorded as having eaten 400 to 900 individuals of the San José scale each day, both the scale itself and the covering being consumed (Fulton, 1915). *O. latipennis* Riley and *O. niveus* DeG. subsist entirely upon insect food, particularly aphids of the genus *Phylloxera*.

MANTIDAE

In both the nymphal and the adult stages, all members of this family subsist upon other insects. The victims comprise almost any insect of a size capable of being overcome, the young nymphs feeding extensively upon aphids, leaf hoppers, etc., and the larger nymphs and adults upon flies, spiders, wasps and bees, grasshoppers, and even beetles. They

tend to frequent flowers, and consequently such insects as are pollen or nectar feeders most frequently fall prey to them. Adult honeybees are frequently killed; in fact, they are stated to be the favorite food of *Tenodera sinensis* Sauss. (Thierolf, 1928). Hadden (1927) gives a list of insects captured by this mantid in Hawaii. All stages are markedly cannibalistic, and the female often devours the male after mating.

In the temperate regions, only a single generation is produced each year, and the winter is passed in the egg state. Several tropical and subtropical species have two generations.

The eggs are deposited in large packets, containing in some species up to 300 to 400 eggs but usually less than 100, upon twigs, grass stems, etc. They are deposited in rows, standing almost vertically, and are enveloped in a frothy mass which quickly hardens into a tough, spongy case. Several hours may be required for the deposition of a single mass. The form of the egg mass is distinctive. It is almost spherical in some species but ranges to the slender mass of *Stagmatoptera septentrionalis* S. & Z. of Panama, which is 6 cm. or more long and only 3 mm. in diameter, and tapers to a fine thread 12.5 cm. long, giving it a marked resemblance to a seed pod.

At hatching, the young nymphs emerge from the egg mass through a series of slits left along the median line on the upper side. They molt almost immediately after leaving the case, and the exuviae is said to be a true skin rather than the amnion. The number of nymphal molts is uncertain, 6 or 7 being recorded for some species and 9 or 10 for others. The females may pass through one more nymphal stage than the male.

An extended account of the biology of a series of Indian species of the family is given by Mathur *et al.* (1934). In *Deiphobe* sp., the hatching of the eggs in each mass extends over a period of several days, in contrast to the almost simultaneous hatching that occurs in most other species of the family.

Litaneutria minor Scudd., which inhabits the more arid regions of North America, has one and possibly two generations each year (Roberts, 1937). Fertile eggs may be deposited within two days after mating, though this is always at least 30 days after the adult stage is reached. Each female may deposit as many as 10 masses of eggs, at intervals of about 10 days, each containing an average of 16 eggs. Overwintering eggs remain unhatched for six to seven months, whereas those deposited in early summer hatch in 30 days. Six to eight nymphal molts occur prior to attainment of the adult form.

The same author's studies (1937*a*) upon *Stagmomantis limbata* Hahn revealed a single generation each year in the same region and the production of 3 to 6 egg masses, containing an average of 65 eggs, at intervals of 14 to 22 days. Oviposition begins not less than 20 days after the final molt.

DERMAPTERA

Occasional species in several families have been found to subsist in part upon other insects. *Chelisoches morio* F. of the South Pacific region is reported to be of considerable importance as an insect feeder, and an examination of the crops of a number of individuals revealed only insect material. In the New Hebrides, it is credited with having a considerable influence in the reduction of the larval population of the hispid beetle, *Brontispa froggatti* Sharp (Risbec, 1933, '35). It also feeds upon the larvae of *Tirathaba*, which is a serious pest of coconut. The caudal forceps are used in attacking the prey and in holding it while it is being consumed. *Spongiphora* sp. has been noted feeding in large numbers upon leaf hoppers on sugar cane in Australia. *Euborellia moesta* Serv. feeds upon codling-moth larvae in France, the nymphs and adults entering the burrows in infested fruit after the latter have fallen to the ground. *Forficula auricularia* L., a common pest in many parts of the world, feeds upon a variety of insects, among them being fleas, which it is able to capture readily. An undetermined species was stated to be the most important natural enemy of the cottony-cushion scale in California prior to the introduction of *Rodolia*. *Labidura riparia* Pall. is reported to be an extensive feeder upon larvae of the cotton worm, *P. litura* F., in Egypt and a single individual may devour 20 medium-sized or 10 large larvae in a single night. Usually, a considerably larger number of larvae are killed than are actually eaten (Bishara, 1934).

THYSANURA

Very little information is available regarding the predaceous habits of members of this order. C. E. Pemberton records the occurrence of an undetermined species, resembling *Lepisma*, in termite nests in Borneo, where they were feeding upon the eggs and young nymphs.

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